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Population characteristics and habitat selection of muskrats (Ondatra zibethicus) in response to water level management at the Summerberry Marsh Complex, The Pas, Manitoba, Canada

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Population characteristics and habitat selection of muskrats *(Ondatra zibethicus)* in response to water level management at the Summerberry Marsh Complex, The Pas, Manitoba, Canada

By

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Chapter 1: General Introduction

The Saskatchewan River drains from the Rocky Mountains in Alberta toward the lacustrine plain of former glacial Lake Agassiz (Morozova and Smith 1999) providing water for a vast expanse of deltaic wetlands in the Saskatchewan River Delta (SRD). The SRD is the largest inland delta in North America, spanning across eastern Saskatchewan and western Manitoba (Land Stewardship Centre of Canada 2010) (Fig. 1). The SRD covers approximately 9950 km^2 (Partners for the Saskatchewan River Basin 2009) and supports a diverse ecosystem that provides natural and economic resources to local native communities through food, fur, and other resources (Lindgren 2001).

Prior to the construction of hydroelectric dams along the river, these wetlands were periodically flooded in early spring and again in mid-summer by high river levels caused by local snow and ice melt and Rocky Mountain snow melt respectively (McLeod 1948). These floods acted as disturbances essential to the wetland wet-dry cycle (van der Valk and Davis 1978, Middleton 1999). However, hydroelectric developments have significantly altered the hydrology, and therefore the wetland cycle, in the SRD by reducing both long term and within year flood frequency (Fig. 2). Extensive wildlife management efforts have taken place in the delta since the 1930's to attempt to mitigate changes in water regime, which affect habitat and wildlife (Smith and Jones 1981). Results of management have made it apparent that this deltaic system is ecologically different than the better studied prairie wetland ecosystem.

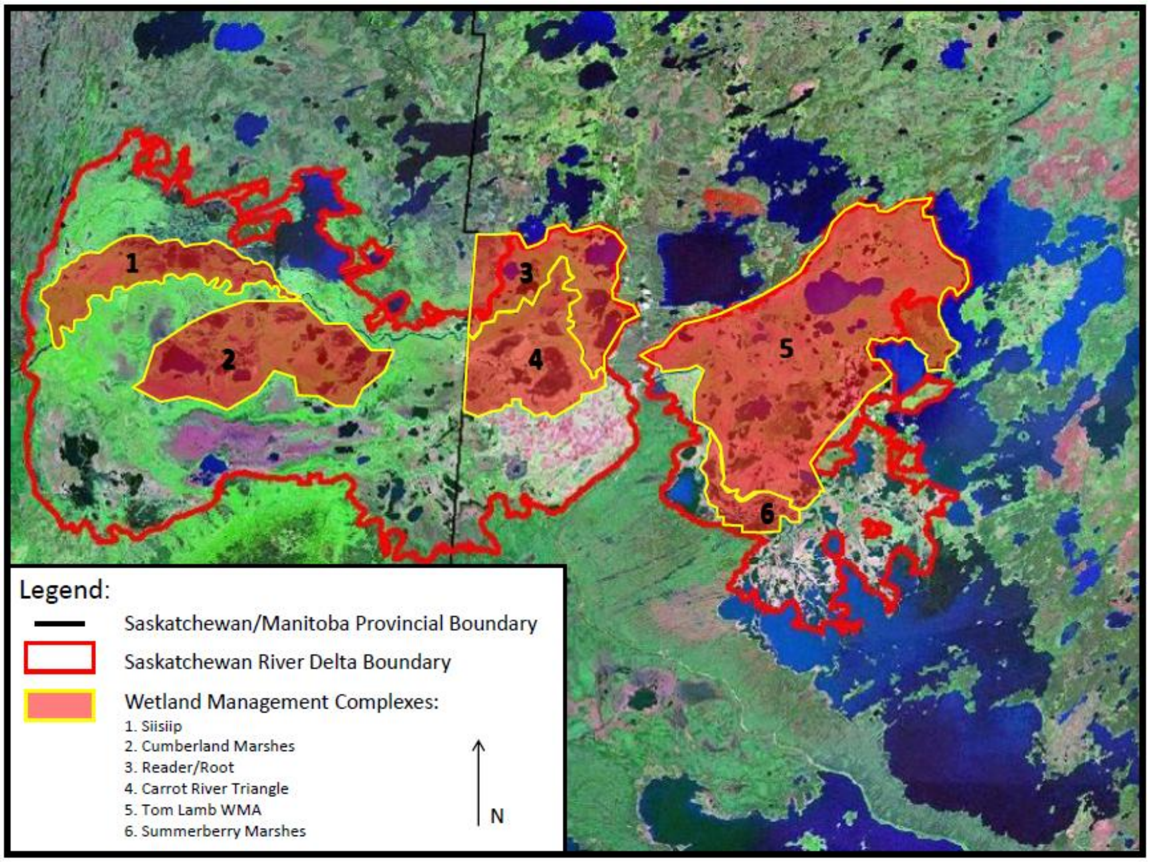

Fig. 1. Map delineating the Saskatchewan River Delta and highlighting six wetland complexes with water level management capability.

The Summerberry Marsh Complex (SMC) is located in the southeastern corner of the SRD, just northwest of Cedar Lake and lying primarily between the Saskatchewan and Summerberry Rivers. This complex is of great value to users of wildlife resources such as muskrats (*Ondatra zibethicus*), moose (*Alces alces*), and waterfowl. In particular, muskrats have historically been of great local interest in the SMC because muskrat farming and local trapping provided fur and meat to local communities and served as an economic staple through the mid twentieth century.

Historic Muskrat Management of the Summerberry Marsh Complex

Portions of the SMC have been managed by Manitoba Conservation, Ducks Unlimited Canada (DUC), and private entrepreneurs since the early twentieth century. Tom Lamb, a private entrepreneur, began constructing levees following the dust bowl of the 1930's specifically for the production for muskrat fur (Smith and Jones 1981). In 1937, what is now Tom Lamb Wildlife Management Area was designated a 'fur bearing animal refuge' (Sexton 1982). In 1942 the Provincial government took over the management of 56,000 hectares in the lower delta for the purpose of rehabilitating muskrat habitat, which had been greatly reduced by the drought of the mid-1930's (McLeod 1950). This muskrat 'farming', a social program run by provincial and federal governments to provide income and food to local people during the post depression era, expanded to 360,000 hectares and was known as the Summerberry Fur Rehabilitation Block (Smith and Jones 1981, Uchtmann 1985, Lindgren 2001).

Water control management goals in the delta from the 1940's through the early 1960's were aimed at water retention and stabilization. The philosophy was said to be 'some water is good, lots would be much better' (Ucthmann, Manitoba Conservation, personal comm.). Myriad dykes, ditches, dams, and water control structures were constructed to impound and retain river flood water in areas that would otherwise be dry for portions of the annual cycle, and therefore would not be quality muskrat habitat.

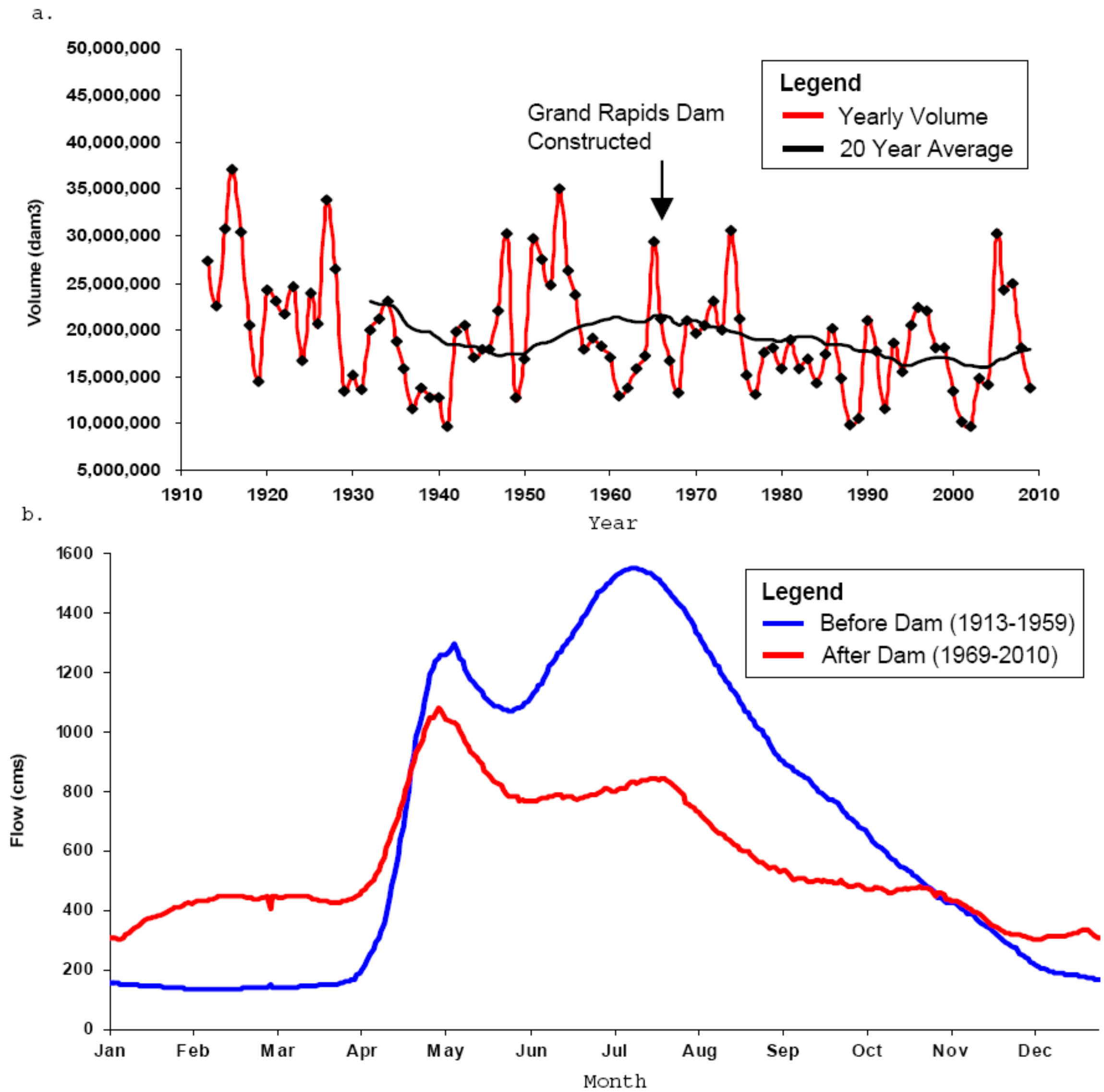

Fig. 2. (a) Total yearly flow of the Saskatchewan River at The Pas, Manitoba, Canada for the past 100 years. (b) Mean weekly flow of the Saskatchewan River at The Pas, Manitoba, Canada before and after dam construction in 1968.

Hydrologic developments on the Saskatchewan River have changed the flow regimes of the river and affected the hydrology of the associated wetlands. In 1964 the construction of the Grand Rapids Hydroelectric dam directly affected the delta by flooding approximately

1/3 of its southern extent into what is now Cedar Lake, covering 1550 km^2 (Lindgren 2001). Large portions of the southern end of the SMC, including the Summerberry Fur Rehabilitation Block, were consequently converted from deltaic wetlands to a permanently flooded lake ecosystem (Uchtmann 1985). The portion of the delta inundated by Cedar Lake was probably the most biologically productive areas of the delta (Harper 1975). Upstream dams now regulate water flow, and the timing of water level peaks, reducing flood frequency (Fig. 2 (a)) and essentially smoothing the hydrograph (Fig. 2 (b)). Leavens (Ducks Unlimited Canada, Winnipeg, personal comm.) predicted over bank flood frequencies will be reduced from one in ten years to one in fifty years. Reductions in flood frequencies and the impoundment of water in SRD wetlands alter the natural ebb and flow in these deltaic wetlands.

It seems the problem of the 1930's of 'not enough water' shifted to a problem of too much water. Clearly the dramatic event was the construction of the Grand Rapids Dam and flooding of the lower delta. However, as early as 1947, Mcleod (1950) recognized signs of vegetation senescence and hence a concomitant decline in muskrat abundance as a result of prolonged high water, and recommended drawdown treatments to reestablish vegetation in degenerating wetlands.

Ducks Unlimited Canada (DUC) took over management of the SMC from Manitoba Conservation in 1979, with the installation of 28 water control structures. The goal during this era was to manage the SMC wetlands for muskrat and waterfowl production through water level manipulation. Active management took place form 1980-1997, but has since been abandoned. In recent years (i.e. since 2005) water levels within the SMC wetlands have been held high following an overbank flood event in the SMC in 2005 (Fig. 2 (a)).

Wetland Ecology and Management

van der Valk and Davis (1978) and van der Valk (2000) outline the well studied wet-dry cycle of prairie wetlands. In the dry marsh stage, drought exposes substrates and the seed bank to oxygen and heat. This facilitates decomposition of plants and remobilizes nutrients previously locked in the substrate. The re-growth of vegetation essentially pumps nutrients from the substrate to above-ground compartments making them available for higher taxa. The return of water floods the vegetation and provides food and habitat for wetland dwelling species. This is the regenerating marsh stage and is presumed to be the most productive stage of the cycle. With prolonged flooding the substrate becomes anoxic and wetland vegetation begins to senesce along with a reduction in population of higher taxa dependent on the vegetation, such as muskrats (Clark 2000). This stage is termed the degenerating stage. If the basin remains flooded, the vegetation will continue to senesce and create open water habitat, referred to as the lake stage. The lake stage is presumed to be the least productive stage in the wetland cycle. A subsequent drought starts the cycle again.

From the 1930's through present, the SMC wetlands can be broadly placed in the stages of the wetland wet-dry cycle. Low water conditions of the late 1930's start the wet-dry cycle in the drought stage. Muskrat populations during this era were low, which spawned interest for water control to increase muskrat populations. Hence the Summerberry Fur Rehabilitation Block was underway by the early 1940's. Water flows in the river increased during the mid-1940's. Higher river flows and the impoundment of water by newly created water works flooded new habitat moving the SMC wetlands into the regenerating marsh stage. This resulted in the highest muskrat abundances in recorded history, as evidenced by muskrat harvest records (Fig. 3). Water flows continued to increase through the 1940's, and the water was impounded, moving the wetlands into the degenerating marsh stage. The muskrat populations of the 1950's and 60's showed a marked reduction from the populations of the 1940's, likely due to prolonged flooding and degenerating wetland conditions. Muskrat populations continued to decline through the 1990's. Present day muskrat populations remain <1/ha in the fall (Ducks Unlimited Canada, unpublished data, 2010), far below the 8 to 50/ha found in prairie wetlands (Errington 1963, Proulx and Gilbert 1983, Clay and Clark 1985, Erb and Perry 2003).

Although some SMC wetlands show signs of the lake stage in the deepest portions of the basins, the vast majority of the habitat remains, at least superficially, in the degenerating stage. This is partially explained by the general morphology of the basins being bowl shaped, where the centers of each basin are the deepest areas, and have moved to the lake stage. In the peripheries, where the water is shallower, emergent macrophytes are present, which conforms to the paradigm of wetland vegetation zonation as a function of depth.

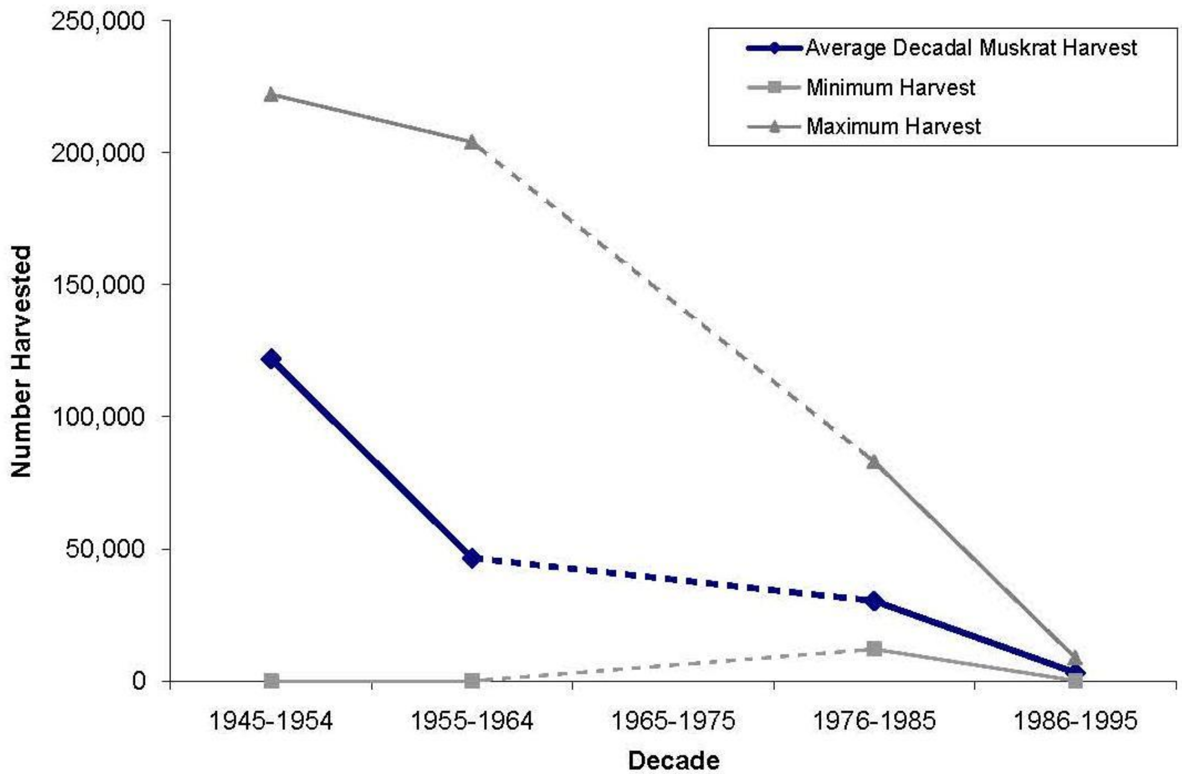

Fig. 3. Muskrat (*Ondatra zibethicus*) harvests by decade in the Saskatchewan River Delta, no point estimates are available for 1965-1975 due habitat changes caused by the closing of the Grand Rapids Hydroelectric Dam and sparse data for that period.

Many wetlands in the SMC, however, do not show signs of lake stages after prolonged flooding. Instead, *Phragmites spp.* continues to grow in water 1 m deep, and *Typha spp.* and *Carex spp.*, among other common emergent macrophytes, grow in floating mats suspended above the substrate. Although no quantitative estimates of aboveground biomass were taken before the flood in 2005, aerial images show no changes in area covered by emergent vegetation from 2007-2009. These apparent differences in flooding tolerances and distributions of emergent macrophytes, along with the floating mats of vegetation in the

SMC wetlands, make it apparent that the ecology of this system differs from that of the prairie wetland system.

Attempts were made by DUC, following the recommendations of Clay (Clay 1978 DUC unpublished report) to implement drawdowns to replicate the natural wet-dry cycle of the commonly studied prairie wetland ecosystem (van der Valk and Davis 1978, van der Valk 2000). This management practice resulted in dense vegetative re-growth which did not senesce after re-flooding, and reduced the habitat quality for waterfowl. Partial drawdowns were implemented instead of complete drawdowns by the mid-1980's in an attempt to limit the re-growth during a drawdown, and prevent re-growth in open water areas with limited success. When compounded with increased regulations on pumping to refill wetlands, the management practice was abandoned in the mid 1990's. When not in use, water control structures act to further stabilize otherwise dynamic water levels.

Muskrat Ecology

Considerably less is known about muskrats in the northern deltaic systems as compared to the prairie ecosystem, although studies have been carried out in the SRD (Mcleod 1948, Phillips 1980) and in the Mackenzie and Peace-Athabaska river deltas respectively (Stevens 1953, Westworth 1974). Muskrat populations have been studied extensively in prairie ecosystems and in the southern portion of their distribution. Studies dating back to Errington's (Errington 1963) study of muskrat populations in Iowa following the dust bowl of the 1930's to the recent studies of the Marsh Ecology Research Program (MERP) at Delta, Manitoba (Clark 2000) have detailed muskrat ecology in prairie wetlands.

Muskrats are short-lived. Mean life span for muskrats is <1 year, with annual survival from birth to one year ranging from 13-16% (Clark 1987, Clark and Kroeker 1993). Overwinter survival is strongly dependent on density and attributes of house location such as water depth and vegetation cover (Errington 1963, Messier et al. 1990, Clark and Kroeker 1993, Virgl and Messier 2000). High muskrat densities increase intraspecific stress and the probability of epizootic disease outbreaks (Errington 1963). Water depth at lodges must be deep enough to prevent freezing all the way to the substrate to allow access to rhizomes and other underground plant parts during the winter. Vegetation can trap snow and act as an insulator reducing ice thickness and preventing freezing of the substrate (Messier et al. 1990, Clark 1994). Houses placed in shallow water zones expose muskrats to predation and winter freeze outs (Clark and Kroeker 1993, Clark 2000) and are presumed to reduce survival.

Muskrat populations are highly productive. Breeding is initiated when waterways become ice free in northern climates (Boutin and Birkenholz 1987). Peak reproductive activity in northern climates tends to be between April and July, but can continue into September (Clark 2000). Muskrats are polyestrous with a 30 day estrous cycle (Wilson 1955, Schwartz and Schwartz 1959). Gestation ranges form 28-30 days and female muskrats come into estrous immediately after parturition (Errington 1963). Muskrats in northern climates have 2-3 litters per year ranging from 4-8 young per litter (Erb and Perry 2003). Neonates are altricial and weigh 15-20 grams at birth (Erb and Perry 2003). They grow rapidly and are weaned at approximately 28 days weighing 150-180 grams (Virgil and Messier 1992, Erb and Perry 2003).

Body condition can affect the ability to survive and reproduce, and understanding how body condition changes over time and in different habitats can lead to valuable insights into population dynamics (Servello et al. 2005). Several methods have been developed for accessing body condition and stress in muskrats. Body condition indices can be derived by dividing body mass by some measure of body size (i.e. body length or leg length) (Clark and Kroeker 1993, Servello et al. 2005). Regressions of mass compared to body length were developed by Virgl and Messier (1995) in central Saskatchewan. Blood parameters relevant to condition, including hemoglobin, hematocrit, and red blood cell counts, were published by MacArthur (1984) derived from muskrats sampled in southern Manitoba.

Muskrat population density varies greatly (Erb and Perry 2003) depending on factors such as season and water level management or fluctuation. Seasonally, lower spring densities are followed by higher fall densities after recruitment. Reported density estimates in prairie wetlands range from <1 to 5/ha in spring, and from 8 to 50/ha in autumn from *Phragmites, Typha,* and *Scirpus* habitats (Errington 1963, Proulx and Gilbert 1983, Clay and Clark 1985, Erb and Perry 2003). Westworth (1974) reported spring densities of 4.0 and 4.8/ha, and, interestingly lower fall densities for both years of the study at 2.8 and 3.5/ha respectively at the Peace-Athabasca River Delta in Northern Alberta. Messier and Virgl (1992) report a maximum fall density of 3.6/ha in central Saskatchewan. Densities at Delta Marsh, Manitoba reached > 30/ha the second growing season following a management drawdown and re-flood, and were consistently lower in May than in October (Clark and Kroeker 1993). Muskrat densities peaked at 7/ha two years after a management drawdown in Lake Erie wetlands (Kroll and Meeks 1985). Toner et al. (2010) found that fall drawdowns to facilitate spring flood control lowered muskrat densities compared to wetlands with 0.7 m higher winter water levels, and that long term water regulation had a negative effect on muskrat densities.

An obvious sign of habitat selection by muskrats is the spatial distribution of lodges which is correlated with water depth and the distribution of various emergent macrophytes (Clark and Kroeker 1993, Clark 2000). Lodges are often located on boundaries between vegetation types (Pelikan et al.1970, Danell 1978, Proulx and Gilbert 1983) potentially due to differences in food quality or preference (Welch 1980, Campbell and MacArthur 1995, 1998) or ability to trap snow. In northern climates water depth at lodges must be deep enough to prevent freezing of the substrate. Vegetation can trap snow and act as an insulator reducing ice thickness and preventing ‘freeze outs’ (Messier et al. 1990, Clark 1994). When ice freezes to the substrate access to rhizomes is restricted and survival is diminished. In prairie wetlands Clark (1994) found that muskrats tend to avoid areas <1 cm deep and the average water depth at lodges was 38 cm. Muskrats tend to avoid deep open water habitats possibly due to increased wave action (Errington 1963), lack of vegetation in close proximity for food and lodge construction, and the inability to build houses in deep water. Conversely, shallow water zones expose them to predation and winter freeze outs (Clark and Kroeker 1993, Clark 2000).

Study Design and Objectives

The past responses of emergent macrophytes to management attempts have made it apparent that this system is ecologically different from the prairie wetland ecosystem on which previous management paradigm has been focused. An understanding and proper management of wetland vegetation will affect muskrat populations. Two generations of local trappers remember, either first or second hand, the high muskrat densities of the 1940’s and compare them with low densities of the recent decades. This disparity provides strong local motivation for the study of muskrats in the SRD.

DUC has therefore renewed efforts to collect ecological data to better understand the dynamics of this system and enlighten management through three studies. In 2007 the study of water quality and vegetation began (Watchorn 2010) and continued through 2008. Waterfowl and secretive marsh bird (Baschuk 2010), and muskrat studies were conducted simultaneously during the summers of 2008 and 2009. The muskrat portion of the study was designed to provide a better understanding of how water level management in the affects muskrat populations in northern deltaic wetlands.

In general terms, field studies were conducted on six wetlands within the SMC. All wetlands have water control structures to facilitate water level manipulation and keep wetlands at desired study levels throughout the duration of the experiment. Wetland manipulation began in the spring of 2007. Three wetlands were partially drawn down (hereafter referred to as PD wetlands), to 30 cm below full supply level (FSL), throughout the experiment, and the remaining three wetlands (hereafter referred to as FSL wetlands) were held at FSL and used as experimental controls (Fig. 4). Wetlands remained at approximately these levels through 2010. Water levels were recorded weekly throughout the summer sampling periods, and data loggers recorded winter water levels, to ensure water levels remained at target levels.

This study focused on understanding the factors influencing muskrat abundance in relation to wetland conditions and management in the SMC. I (1) assessed trends in muskrat populations in the study wetlands through mark-recapture trapping, (2) analyzed muskrat house placement in relation to physical wetland characteristics through logistic regression modeling to create resource selection functions, and (3) analyzed historical aerial house counts, conducted by DUC, to assess trends in muskrat house abundance in relation to time, weather conditions, and water level management.

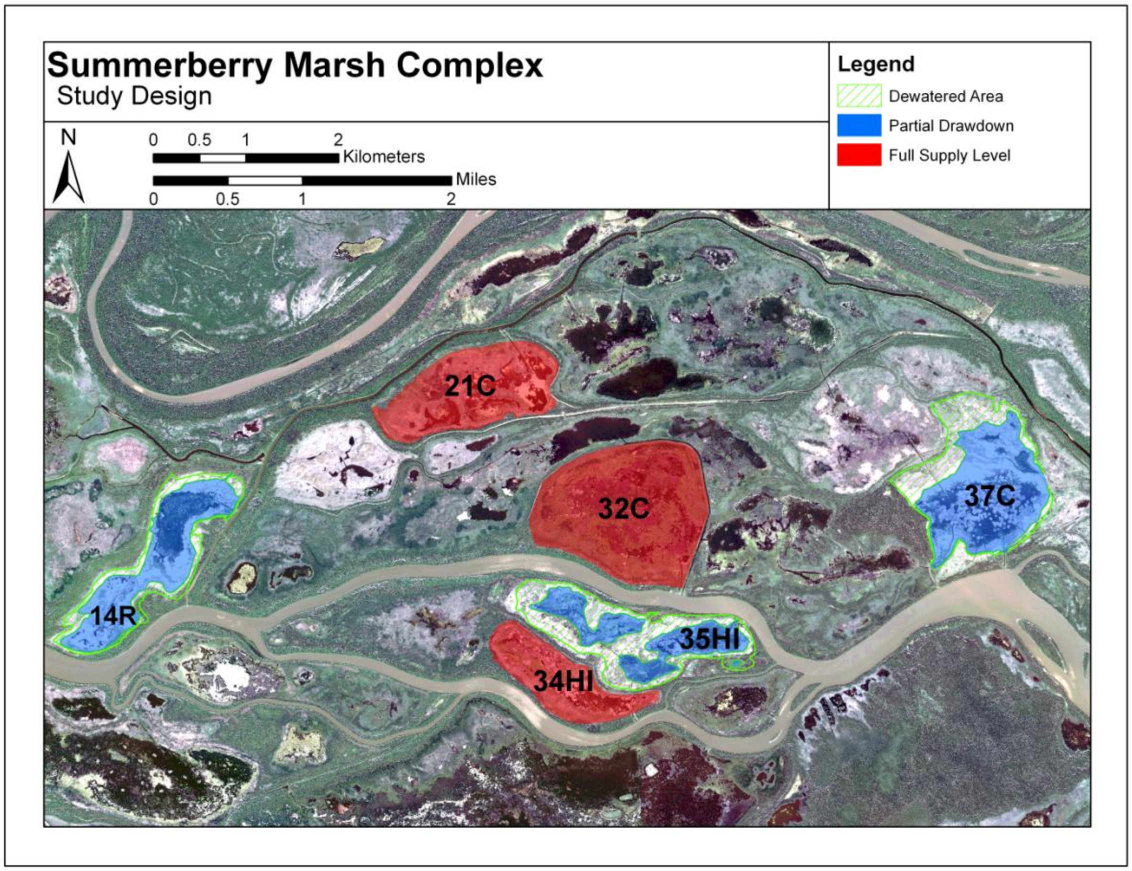

Fig. 4. Study design displaying full supply level (FSL) and partial drawdown (PD) wetlands, as well as the area dewatered by the partial drawdown, at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

Thesis Organization

This thesis consists of a general introduction chapter (Chapter 1), three chapters (Chapters 2-4) prepared for submission to The Canadian Journal of Zoology, and a chapter of general conclusions (Chapter 5). References cited in Chapters 1 and 5 are provided after Chapter 5. This thesis was written by Michael Ervin and edited by William R. Clark.

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CHAPTER 2: POPULATION AND PHYSIOLOGICAL RESPONSES OF MUSKRATS (*Ondatra zibethicus*) TO WATER LEVEL MANIPULATION AT THE SUMMERBERRY MARSH COMPLEX, THE PAS, MANITOBA.

A paper submitted to the Canadian Journal of Zoology

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Abstract

I studied muskrat (*Ondatra zibethicus*) populations in response to a partial (30 cm) late summer drawdown in the Saskatchewan River Delta, Manitoba, Canada, 2007 through 2009. I conducted house counts from airboats in 2008, 2009, and 2010 to assess house density. I live trapped muskrats in 2008 and 2009 to estimate population size, using closed population models, and to assess muskrat density and body condition. I assessed body condition in 2009 using three techniques, body condition indices (BCIs), hematocrit, and neutrophil to lymphocyte (N/L) quotients. Muskrat house densities were lower partial drawdown (PD) wetlands than full supply level (FSL) wetlands one year following the drawdown. Conversely, muskrat densities, derived from mark-recapture sampling, showed no indication of reduced population densities in PD wetlands. BCIs were unaffected by the partial drawdown, and the ANOVA model constructed to test for differences in hematocrits was not significant indicating no differences between treatments. N/L quotients were higher in PD wetlands, and in the spring indicating the partial drawdown and overwinter conditions may have induced physiological stress.

Introduction

Muskrat populations have been well studied in prairie and estuarine ecosystems, however less is known about the ecology and management of muskrats in northern deltaic ecosystems. Although research on muskrat populations has been carried out in the Saskatchewan River Delta (SRD) (Mcleod 1948, Phillips 1980) and in the Mackenzie and Peace-Athabaska river deltas (Stevens 1953, Westworth 1974), to my knowledge muskrat population response to management drawdowns has not been studied in such northern deltaic ecosystems.

Water regime affects muskrat populations (Erb and Perry 2003) and differs between northern deltaic wetlands and prairie wetlands, to which they are often compared. The Saskatchewan River traditionally flooded at The Pas, Manitoba bi-annually (Fig. 1a) once following local ice melt in early spring, and again in July when water from the Rocky Mountain snow melt arrived. Such rapid fluctuations in water levels can displace muskrats and make habitat unsuitable. Rapid rises in wetlands inhabited by muskrats can flood houses and displace muskrats. Conversely, rapid reductions in water levels, or droughts, can also make habitat unsuitable for muskrats. Water regimes of deltaic wetlands are inherently dynamic; therefore sustaining high muskrat populations and yearly fur yields is difficult if water levels are not managed. In the 1930's, economic stress and the relatively high value of muskrat fur prompted interest in habitat manipulation designed to promote muskrat production in the SRD (Ucthmann 2008).

Myriad dykes, ditches, and water control structures were built in portion of the SRD known as the Summerberry Marsh Complex (SMC) during the 1940's to stabilize the unregulated water levels of the Saskatchewan River in SRD wetlands primarily for muskrat production. These water control structures impounded and stabilized water on newly regenerated wetland habitats which had been dry during the drought of the late 1930's (Fig. 1b), and muskrat populations boomed (Fig. 2). McLeod (1950) studied muskrat populations in the SMC at this time using winter house counts. He documented an increase in muskrat populations in the SMC following the construction of water control structures, and a subsequent decline in populations through the 1950's that has apparently continued to the present. Data from aerial house counts conducted in winter 2008 suggests muskrat densities in the SRD to be <1/ha (Ducks Unlimited Canada, unpublished data, 2010). Though not directly comparable, these current population estimates are considerably lower than estimates from McLeod (1950), and from densities reported in prairie ecosystems (Errington 1963, Proulx and Gilbert 1983, Clay and Clark 1985, Erb and Perry 2003).

Today, hydroelectric developments on the Saskatchewan River have reduced the frequency and magnitude of flood events at The Pas, Manitoba (Fig. 1), and the SRD. Reductions in the magnitude of flooding have reduced the frequency of overbank flood events, which historically inundated wetlands with river flood water. This fact, in combination with increased cost and strict regulations on pumping, have made managers reluctant to draw down wetlands, in fear of not having the resources (i.e. water, or money to pump water) to reflood. Therefore, the water control structures designed to enable draw downs, which regenerate wetland habitats, now impound water promoting degenerating wetland conditions throughout the SRD. Long term water level regulation, as apparent in the SRD, reduces wetland productivity and muskrat abundance (McLeod 1950, van der Valk and Davis 1978, Erb and Perry 2003, Toner et al. 2010).

Water level manipulation is the primary muskrat management technique (Erb and Perry 2003). Muskrat populations respond to natural fluctuations in water level (Errington 1963, Clay and Clark 1985, Erb and Perry 2003) and water level manipulations imposed by managers (Clark 2000, Erb and Perry 2003, Toner et al. 2010). This is primarily because periodic droughts, or managed drawdowns, can recycle nutrients (Murkin et al. 2000b) and stimulate emergent vegetation used by muskrats as food or to build houses (Weller and Frederickson 1973, Clark 2000). Ninety nine water control structures are present in the SRD, 28 of which are in the SMC (Robin Reader, Ducks Unlimited Canada, The Pas, pers. communication 2010). These control structures provide varying degrees of water level manipulation capability, from complete drawdown in some wetlands, to partial drawdown in others.

Though not studied in northern deltaic systems, muskrat population responses have been well studied in prairie ecosystems providing a basis for hypotheses testing about our study system.

Population responses to drawdowns

Although beneficial in the long term, drawdowns can result in complete elimination or partial reduction in muskrat populations during the drawdown (Errington 1961, Clark 2000). Upon reflooding rapid invasion of new habitat is typical, and muskrat populations appear to reach peak population levels 3-5 years following reflooding (Kroll and Meeks 1985, Clark and Kroeker 1993, Clark 2000). Muskrat densities at Delta Marsh, Manitoba reached > 30/ha the second growing season following a management drawdown and re-flood

(Clark and Kroeker 1993). Toner et al. (2010) found that fall drawdowns designed to facilitate spring flood control lowered muskrat densities compared to wetlands with 0.7m higher winter water levels, and that long term water regulation had a negative effect on muskrat densities.

Recruitment

Reproductive rates vary following management drawdowns (Beer and Truax 1950, Kroll and Meeks 1985, Clark and Kroeker 1993) and should be understood by managers. In northern climates reproduction initiates when wetlands become ice free, and adult females have 2-3 litters per year ranging from 4-8 young per litter (Erb and Perry 2003). McLeod (1950) reported juvenile to adult female ratios of SMC muskrats ranging from 6.8-12.0, though his methods were not explicitly documented. Recruitment is density dependent (Errington 1963, Clark and Kroeker 1993, Clark 2000). It is also dependent on habitat quality, particularly the combination of water depth and vegetation types. At Delta Marsh, Manitoba, Clark and Kroeker (1993) related differences in recruitment between wetlands receiving varying water level treatments to the initial vegetation response to a drawdown. They noted an increase in recruitment in the first two years following a drawdown, but then recruitment dropped, regardless of treatment, after three years of reflooding as wetland vegetation began to senesce.

Body Condition

Body condition can affect the ability to survive and reproduce (Servello et al. 2005), and therefore the effects of a management practice on body condition should be understood. Clark and Kroeker (1993) found that muskrat body condition indices (BCIs) (i.e. body weight/body length) were inversely proportional to population density, and also that BCIs did not differ among adults in response to water level manipulation. BCI’s, however, are insensitive to seasonal changes in physiological condition.

In contrast, hematocrit assesses the proportion of red blood cells in whole blood, and is sensitive to seasonal changes in physiology. Red blood cells carry oxygen to peripheral body parts. Since muskrats are semi-aquatic divers and oxygen is often limited, reductions in hematocrit values, anemia, could limit the oxygen affinity of blood therefore reducing the ability to perform long dives under the ice to gather food in winter (MacArthur 1984b). Indeed, MacArthur (1984a) examined hematocrits of summer and winter acclimatized muskrats and found hematocrit values to be higher in winter presumably to cope with long dives under the ice and increased CO_2 levels caused by huddling in houses.

Another sensitive approach to assessing physiological condition is measuring neutrophil / lymphocyte quotients. Glucocorticoid levels increase in response to exogenous stressors and increase the neutrophil / lymphocyte quotient of peripheral blood, therefore increased N/L quotients reliably indicate increased levels of stress hormones. This phenomenon is conserved across vertebrate taxa, and the method is not dependent on rapid sampling techniques (Davis et al. 2008), and therefore well suited use with captured muskrats.

Muskrats play an important role in wetland ecosystems; therefore an understanding of how muskrat populations respond to water level manipulation is essential in understanding the ecology and management of any wetland ecosystem in which they are present or desired. Local interest in muskrats as a food, fur, and recreational resource have prompted interest in understanding how muskrat populations respond to water level management in the SMC, and more generally the SRD. My study was part of a larger study to assess the effects of water level manipulation on water quality and vegetation (Watchorn 2010), secretive marsh birds and waterfowl (Baschuk 2010), and muskrats (Ervin 2011). My objectives were to assess (1) muskrat abundance and density, (2) recruitment, and (3) body condition in response to water level manipulation in northern deltaic wetlands. My intent was to provide managers with an understanding of how muskrat populations respond to water level manipulation in northern deltaic wetlands, specifically in the Saskatchewan River Delta at the Summerberry Marsh Complex (SMC).

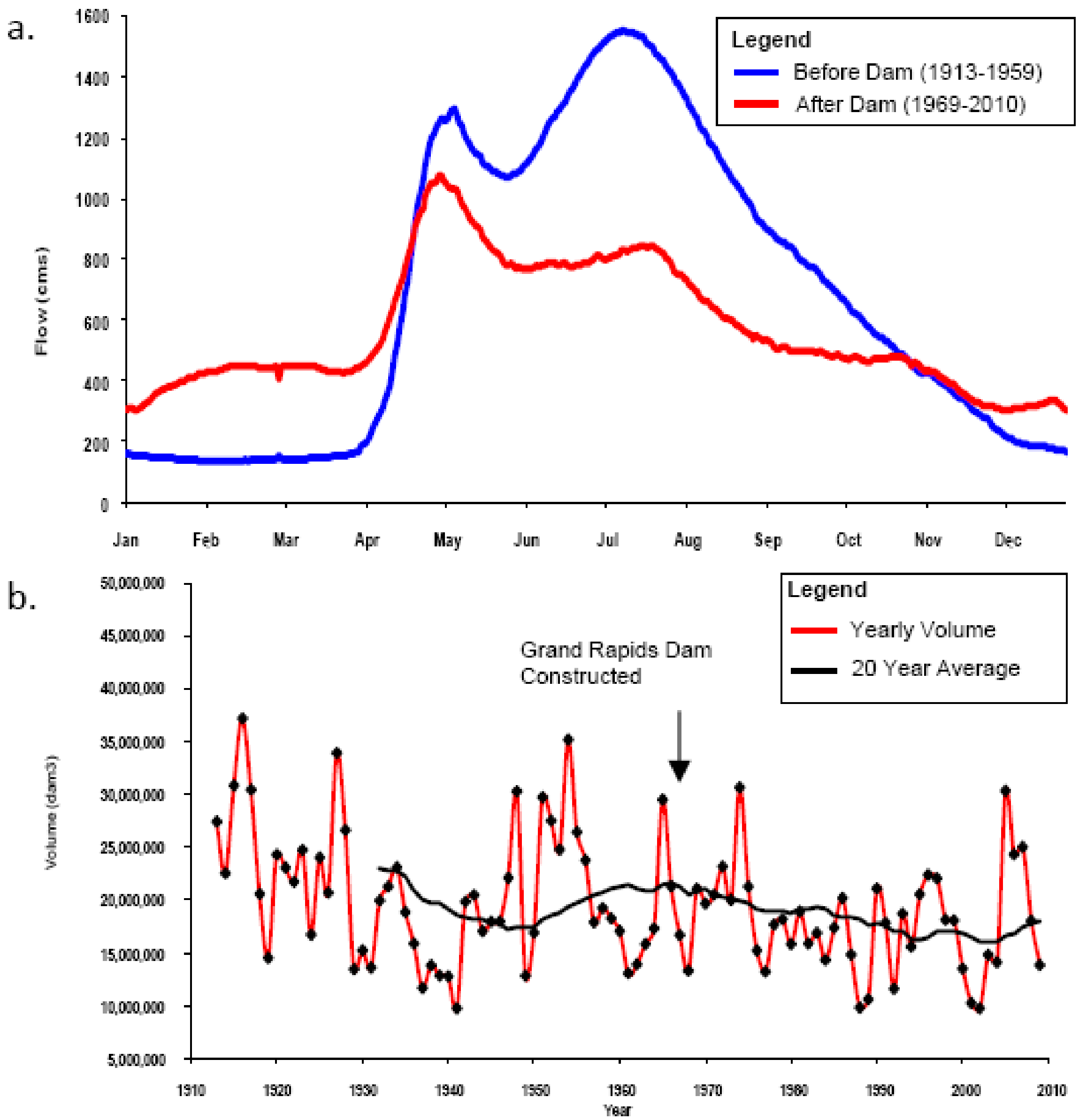


Fig. 1. (a) Mean weekly flow of the Saskatchewan River at The Pas, Manitoba, Canada before and after the construction of the Grand Rapids Dam in 1968. (b) Total yearly flow of the Saskatchewan River at The Pas, Manitoba, Canada for the past 100 years.

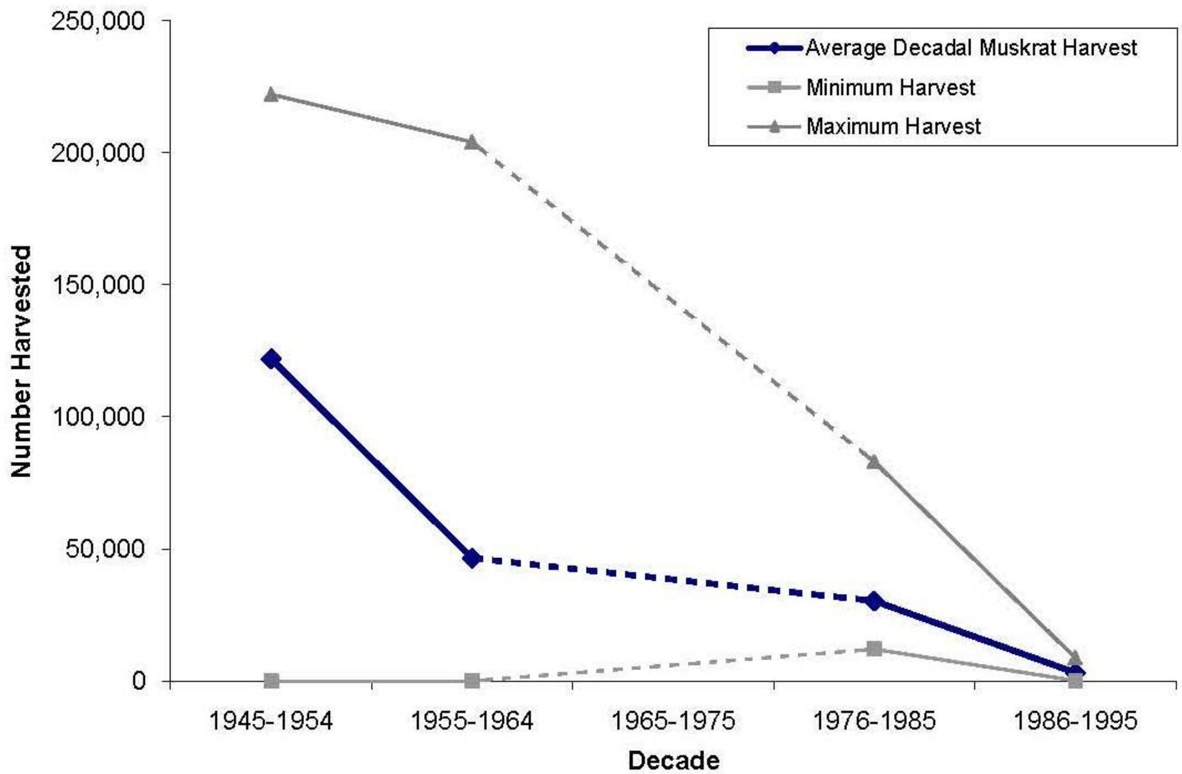


Fig. 2. Muskrat (*Ondatra zibethicus*) harvests by decade in the Saskatchewan River Delta, no point estimates are available for 1965-1975 due habitat changes caused by the closing of the Grand Rapids Hydroelectric Dam and sparse data for that period.

Study Area

The SMC is located in the southeastern corner of the SRD, approximately 24 km downstream of The Pas, Manitoba, Canada. The SMC encompasses 14,000 ha, of which approximately 7,000 ha are wetlands, downstream from the head of the Summerberry River to the delta at Cedar Lake. Ducks Unlimited Canada (DUC) manages 28 control structures within the SMC, capable of a range of water level manipulation from full supply level to complete drawdown. Control structures in the SMC were built in 1978, and active water level management occurred from 1979-1990. No managed drawdowns have occurred in the SMC since 1990. Annual daily mean temperature at The Pas, Manitoba from 1971-2000 was 0.1°C, and 162 days per year had a snow depth of at least 1cm (Environment Canada, 2010).

The research group selected six study wetlands based on location, size, and ease of access and water level. At the time, of study dense emergent vegetation primarily composed of sedges (*Carex spp.*), horsetails (*Equisetum spp.*)¸reed grass (*Phragmites australis*), cattails (*Typha spp.*), and bulrushes (*Scirpus spp.*) dominated the emergent zone of the study wetlands. Open water habitat was present in the deeper central portion of each study wetland, and also interspersed with vegetation toward the periphery of the wetlands. The maximum depth recorded in any study wetland was 145 cm.

Methods

Water Level Manipulation

Each of the six study wetland has a water control structure to facilitate water level manipulation and control. Water level manipulation began in the spring of 2007. Partial drawdowns, to approximately 30 cm below full supply level (FSL) (i.e. maximum legal water level), were implemented on the three ‘partial drawdown (PD)’ wetlands; 14R, 35HI, and 37C. The remaining three ‘full supply level (FSL)’ wetlands, 21C, 34HI, and 32C, were held at approximately FSL and designated as experimental controls (Fig. 3). Wetlands remained at approximately these levels through 2010 (Appendix A). Water levels were recorded weekly throughout the summer sampling periods, and data loggers recorded winter water levels, to ensure water remained at target levels.

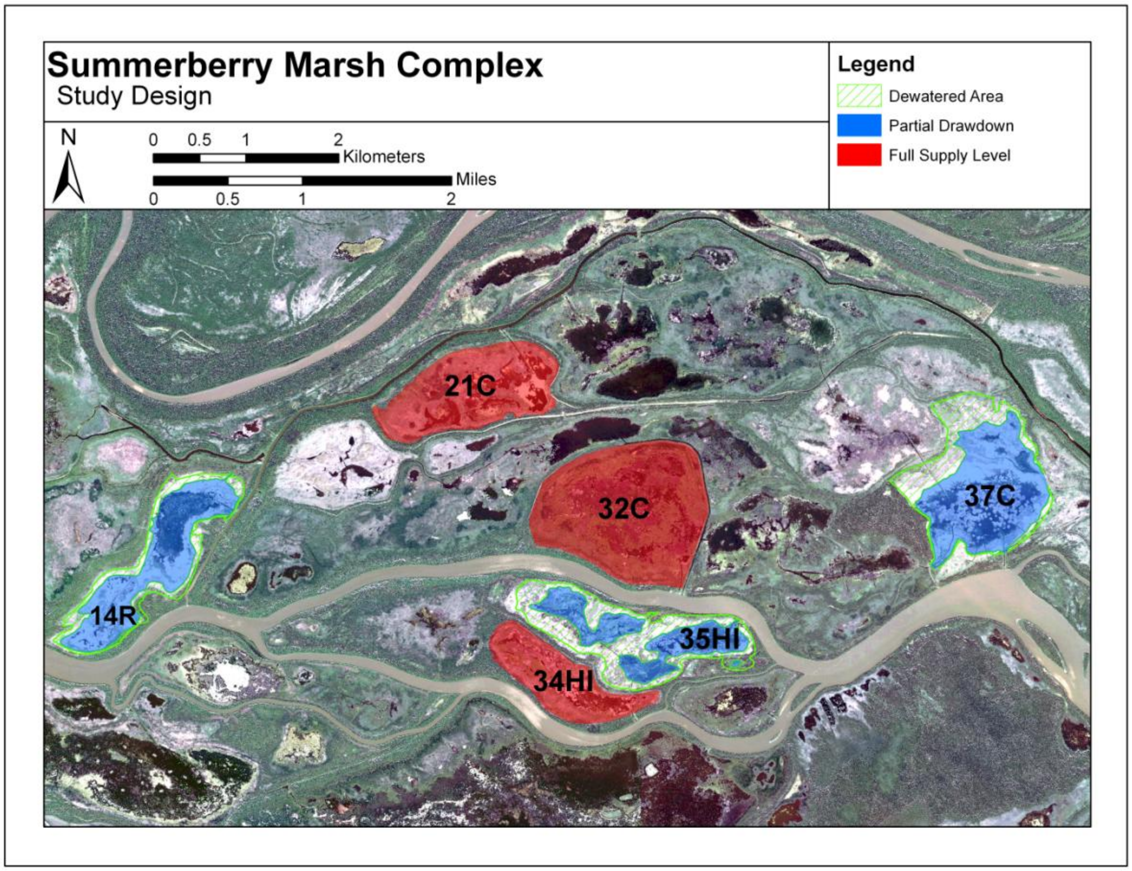


Fig. 3. Study design displaying full supply level (FSL) and partial drawdown (PD) wetlands, as well as the area dewatered by the partial drawdown, at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

House Counts

I conducted house count surveys from air boats in June 2008, June 2009, September 2009, and June 2010. House count surveys were conducted in each wetland 2-3 days before mark-recapture surveys. I conducted surveys on transects that were spaced approximately 40 m apart and covered the entirety of each study wetland (Fig. 4). I stopped the airboat at each house or feeding platform in order to mark the location with a Garmin GPSMap 76c, measure water depth to the nearest centimeter, record dominant vegetation, and assess activity. I designated all muskrat structures that were conical in shape and constructed of cut emergent vegetation as houses. I designated an object as a feeding platform if it had a flat upper surface and was constructed of emergent vegetation. Although I did not measure the height of each house, houses were generally taller (i.e. 30-150 cm above water surface) than feeding platforms (i.e. 5-10 cm above water surface). Houses and feeding platforms were designated as active in spring surveys if they appeared to be built the previous fall (i.e. houses 60-150 cm above water surface), or in surveys after green up if freshly cut, green vegetation was present. Additional areas of activity, such as muskrat runs, beaver houses, beaver slides, etc, were marked for use in trap site selection, but not recorded as houses or feeding platforms. For analysis purposes I considered house count surveys to be a census of all muskrat houses present during each sampling period. I calculated house density by dividing the house count for each sampling period by the FSL surface area of each wetland.

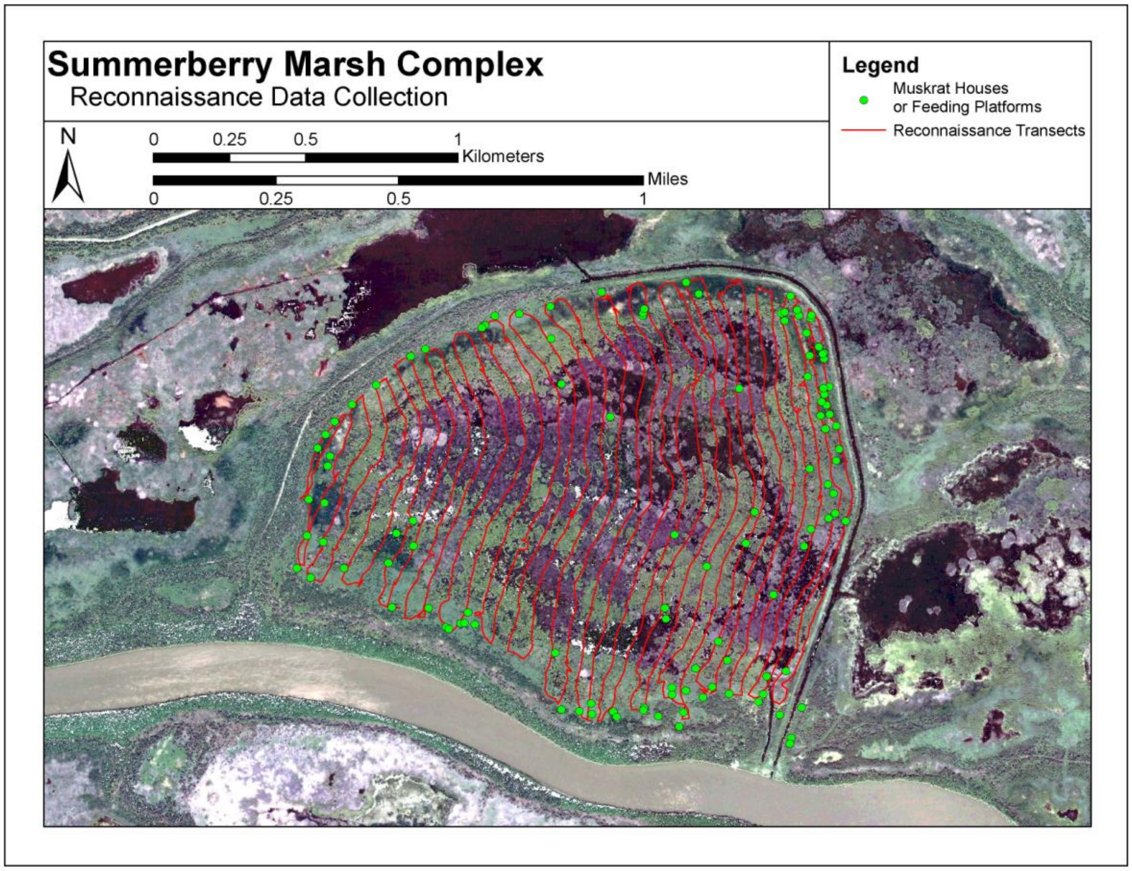


Fig. 4. Survey carried out in wetland 32C prior to mark-recapture sampling on 23 June 2009 to locate muskrat (*Ondatra zibethicus*) houses at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

Mark-Recapture Surveys

I set Tomahawk model 202 (48 x 15 x 15 cm) live traps at active houses, feeding platforms, runs, or other areas with muskrat sign that were marked during house count surveys to maximize capture probability. Each trap was covered with surrounding vegetation to provide shade to captured animals and aid in trap concealment. I baited traps with an apple slice or commercial scent to entice muskrats to enter the trap. I checked traps daily and all animal handling followed approved Iowa State University Institutional Animal Care and Use Committee procedures (#4-08-6533-W) under Manitoba Wildlife Scientific Permit WB07955.

Upon capture, I transferred captured muskrats from the trap to a handling cone. I marked all individuals using Monel 1005-1 ear tags in each ear and a waterfowl style leg band (size 1242-10) around one hind leg proximal to the ankle joint. I recorded sex, weight, body length, hind foot length, age, location of capture of each individual, and drew blood from each captured individual in June 2009 and September 2009. Sex was determined by examining external genetailia. Body weight was measured with a spring scale by weighing muskrats in the handling cone, and then removing the muskrats and weighing the handling cone, then subtracting the difference. I measured adults to the nearest 25 g, and juveniles to the nearest 5 g. Body length was measured to the nearest centimeter dorsally from the tip of the nose to the tail base. Hind foot length was measured in millimeters, on the ventral side of the foot, from the base of the heel to the tip of the flesh on the longest toe. Age was determined as adult or juvenile (young of the year) in the field by fur color, or weight when the fur of older juveniles had turned brown. An individual was classified as a juvenile if it had grey fur, or if its weight ranged from 125-650 g; or as an adult if fur was brown and weight ranged from 675-1300 g.

Each study wetland was trapped once in 2008 and twice in 2009. In 2008 I trapped for seven nights with 50 traps from 15 May – 31 July; hereafter I refer to this sampling period as June 2008. Based on the 2008 data, I changed trapping designs in 2009 in an attempt to (1) increase sample sizes and (2) to sample both spring and fall to aid in survival and recruitment estimation as outlined in Pollock's robust design (1990). In 2009 I trapped each wetland for four days with 70 traps per wetland. Spring sampling was conducted from 18 May - 22 June, hereafter referred to as June 2009, and fall sampling took place from 15 August – 26 September, hereafter referred to as September 2009. I did not conduct mark-recapture surveys in 2010 due to small sample sizes in September 2009.

Population Estimates

I used a combination of house counts (Dozier 1948) and mark-recapture data (Otis et al. 1978) to assess trends in muskrat abundance. From house counts I report the total number of active houses marked and houses per hectare for each sampling period to assess trends in abundance. For house count surveys, I calculated houses per hectare by dividing the number of houses marked during each survey by the full supply level area of each wetland. I calculated the full supply level area from topographic ground surface contours and full supply water levels provided by DUC. I then used the cut/fill tool in the ESRI ArcMap 3d Analyst extension to subtract the ground surface elevation from the water surface elevation. I used areas in the resulting raster with negative values as the full supply level area for each wetland.

I used program CAPTURE (White et al. 1982) to derive closed population estimates (Otis et al. 1978) in each wetland. I tested mark-recapture data from each wetland for closure. Where sample sizes were sufficiently large I used mark-recapture data to estimate population size ($\hat{N}$) and 95% confidence intervals, for each study wetland during each sampling period. When sample sizes were insufficient for estimation I reported the number of captures (M_{t+1}) (Otis et al. 1978). I report naïve muskrat density, without correcting for edge effects, for each sampling period using $\hat{N}$, if attainable, or M_{t+1}. For mark-recapture surveys, I calculated naïve population density by dividing $\hat{N}$ or M_{t+1} for each sampling period by the flooded surface area of each wetland. I calculated the flooded surface area from topographic contours and water levels collected by the research team during study. I used the cut/fill tool in the ESRI ArcMap 3d Analyst extension to subtract the ground surface elevation from the water surface elevation. I used areas in the resulting raster dataset with negative values (i.e. areas where the water surface elevation was greater than the ground surface elevation, and thus represented flooded areas) as the flooded surface area for each wetland. I used a slightly different method to calculate naïve population density compared to house density. For the naïve population density estimates I used the actual water levels, therefore in PD wetlands the area dewatered by the drawdown (Fig. 3) is not represented in the naïve density estimates since that area was not sampled during mark-recapture surveys.

I compared house density per hectare, population estimates, and naïve population density between FSL and PD wetlands in an analysis of variance (ANOVA) with water level treatments (individual wetlands nested within) and sampling period as main effect terms using Jump 8.0 software (Sall et al. 2001).

Recruitment

Because of no trapper effort, removal trapping in the study wetlands did not occur during the study period. Therefore, I estimated recruitment from carcasses collected from other areas of the SRD trapped during the legal harvest seasons, October through May 2008-2010.

To estimate age I followed the molar fluting index methods outlined by Erb et al. (1999). I collected heads from each carcass, froze them, and transported them to Iowa State University for further processing. I thawed and boiled heads to facilitate the removal of the lower right molar. Then I used digital calipers to measure the total tooth length from the anterior tip of the root to the anterior most point on the occusal surface to the nearest 0.01mm. I then measured flute length from the tip of anterior most flute to the anterior most point on the occusal surface. I calculated molar indices by dividing total length by flute length. I classified carcasses into age classes using molar index cut-off values placed between peaks in frequency histograms of molar index values.

To estimate juvenile to adult female ratio, a measure of recruitment, I used the age class estimates I derived from the carcasses gathered from local trappers. Additionally, I dissected reproductive tracts from all female carcasses and counted placental scars to estimate pregnancy rate of adult females, and to calculate an average number of placental scars per pregnant female. Pregnancy rate was derived by dividing the total number of adult females with >1 placental scar, by the total number of adult females in the sample of carcasses.

To estimate birth dates and litter frequency I back-dated age estimates of all live captured young of the year. I estimated age in days of all young of the year by using the age-weight regression

[1] $$AGE = 0.157 \times Bodymass(g) - 1.114$$

published by Virgil and Messier (1995). I estimated the numbers of litters from peaks in estimated birth date frequencies (Clay and Clark 1985). Additionally, I estimated the onset of breeding by assuming gestation period of 29 days (Errington 1963).

Body Condition

I calculated body condition indices (BCIs) of muskrats caught in June 2008, June 2009, and September 2009 using the following formula:

[2] $$BCI = \frac{BodyWeight\,(g)}{BodyLength\,(cm)}$$

(Clark and Kroeker 1993, Servello et al. 2005).

I drew blood samples from the saphenous vein (Diehl et al. 2001) at the time of first capture to analyze hematocrit and neutrophil / lymphocyte quotients of muskrats caught in June 2009 and September 2009. To draw blood I shaved a small portion of the leg from which blood was to be drawn. I applied Vaseline® to the area to make the vein more visible and prevent blood mixing with water. I punctured the saphenous vein with a 20 gauge needle and collected blood in a hepranized capillary tube. A small portion of the sample was immediately transferred to a slide to make blood smear slides. Residual blood was stored in the capillary tubes. Capillary tubes were plugged with CritSeal® and stored on ice until they were further processed 0-4 h from time of collection.

Blood stored in capillary tubes was used to measure hematocrits. Hematocrit is the volumetric proportion of packed red blood cells to the amount of whole blood in a sample. I spun capillary tubes in an International Clinical Centrifuge for two minutes and measured hematocrits from the total volume of blood to the nearest 0.5mm.

Blood smear slides were fixed in methanol and stained in Wright-Giesma stain by the Veterinary Pathology Department Iowa State University to facilitate the identification of white blood cells. We counted 100 white blood cells from each blood smear slide and classified them as neutrophils, lymphocytes, monocytes, basophils, or eosinophils. Two observers were used to independently count 97 of 110 (88%) of slides. In 13 of 110 (12%) slides two observers independently counted white blood cells from the same fields of view.

I built separate ANOVA models for body condition indices, hematocrit, and neutrophil / lymphocyte quotients. Each model contained main effects parameters for water level treatment, sampling period, sex, and age, and an interaction parameter sampling period*treatment. For blood slides counted independently by two observers I used one-way ANOVA to test the results for observer bias.

Results

House Counts

I marked 462 active and 833 inactive houses in four sampling periods, June 2008, June 2009, September 2009, and June 2010. I used only active houses in analysis and excluded inactive houses and feeding platforms since they were not inhabited by muskrats and therefore not informative about abundance. There appeared to be a decline in the number of muskrat houses during the study (Fig. 5, Table 1). Muskrat house density differed among treatments ($F_{[1, 15]}$ = 6.01, P = 0.027) and densities in PD wetlands were lower than in FSL wetlands ($t_{[1]}$ = -2.24, P = 0.04) indicating a negative effect of the drawdowns on house density (LS means Table 1). House density differed among sampling periods ($F_{[3, 15]}$ = 5.95, P = 0.007) and was highest in June 2009 and lowest in September 2009. Compared to the reference category June 2008, house densities in June 2009 were higher ($t_{[3]}$ = 3.12, P = 0.007), while September 2009 ($t_{[3]}$ = -1.9, P = 0.08) was marginally lower, and June 2010 was lower ($t_{[3]}$ = -2.3, P = 0.04) (LS means Table 1).

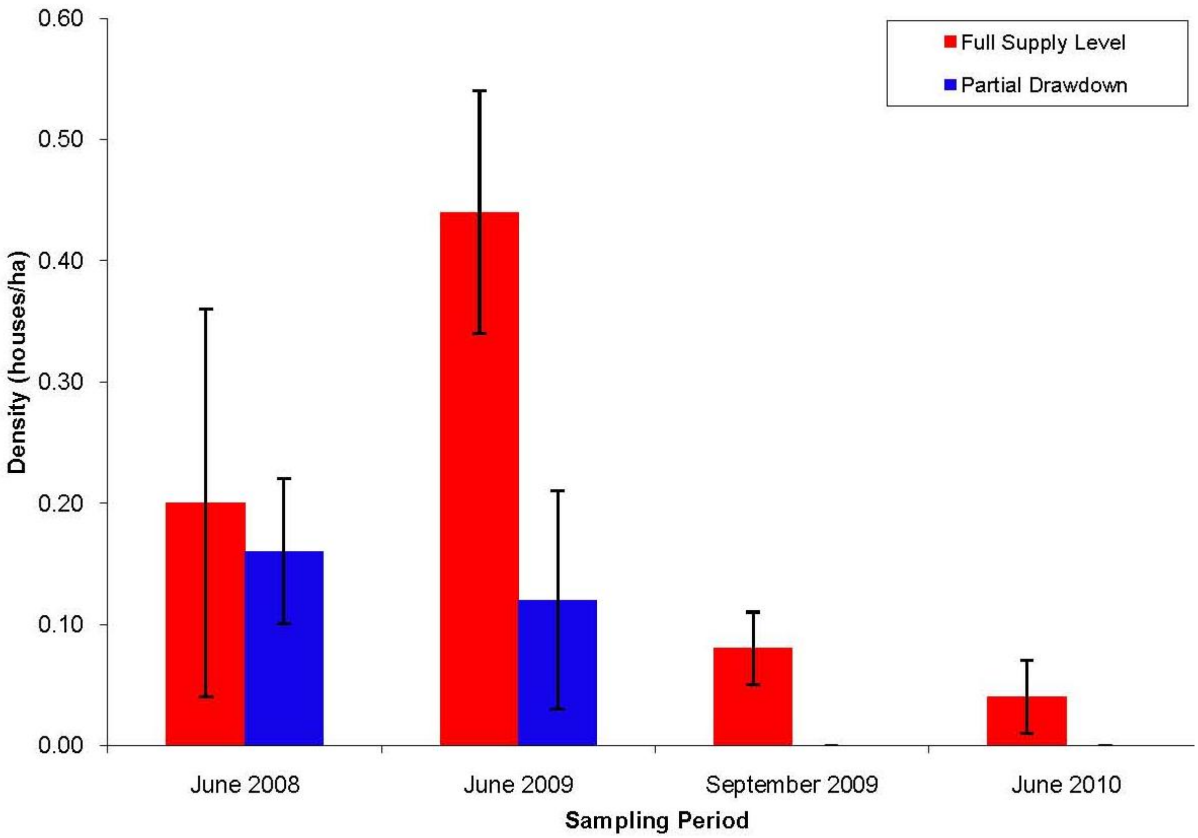


Fig. 5- Average density of active muskrat (*Ondatra zibethicus*) houses per hectare, and 95% confidence intervals, in full supply level (n = 3), and drawdown (n = 3) wetlands during June 2008- June 2010 at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

Table 1: Counts (n) of active muskrat (*Ondatra zibethicus*) houses and house density per hectare (D/ha) June 2008 - June 2010 at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

			Full Supply Level		Partial Drawdown			Least Square Means	
Sampling Period			$\bar{x}$	SE	$\bar{x}$	SE		$\bar{x}$	SE
June 2008	**n**		29.33	23.33	24.66	8.95			
	D/ha		0.20	0.16	0.16	0.06		0.18	0.06
June 2009	**n**	*	61.33	11.29	18.33	13.83			
	D/ha	*	0.44	0.10	0.12	0.09		0.28	0.06
September 2009	**n**	*	14.00	6.02	0.00	0.00			
	D/ha	*	0.08	0.03	0.00	0.00	†	0.04	0.06
June 2010	**n**		6.33	4.84	0.00	0.00			
	D/ha		0.04	0.03	0.00	0.00	†	0.02	0.06
Least Square Means		‡	0.19	0.04	0.07	0.04			

*** - denotes levels where arithmetic means were significantly different ($p < 0.1$) between Full Supply Level and Partial Drawdown wetlands**

† - denotes levels where least square means were significantly different ($p < 0.05$) from the June 2008 sample

‡ - denotes least square means that were significantly different between Full Supply Level and Partial Drawdown wetlands

Population Estimates

Over all sampling during June 2008, June 2009, September 2009 I captured a total of only 331 muskrats. Small sample sizes made population estimation and comparisons between PD and FSL wetlands difficult. Captures and recaptures were sufficient to estimate $\hat{N}$ and SE($\hat{N}$) using closed models in four wetlands in June 2008. In all other sampling periods captures and recaptures were too small to estimate $\hat{N}$, so I report M_{t+1} (Fig. 6).

Naïve spring breeding density estimates ranged from 0.31/ha (SE 0.06) in June 2008 through 0.1/ha (SE 0.06) in June 2009 across both treatments and average naïve density estimate in September 2009 was 0.12/ha (SE 0.06) (Fig. 7, LS means Table 2). I did not detect an effect of treatment ($F_{[1, 10]} = 0.685$, $P = 0.436$) on population densities, likely because of the consistently low densities in June and September 2009. Differences among sampling periods, however, were significant ($F_{[2, 10]} = 7.33$, $P = 0.01$). The June 2008 sample was significantly higher than the September 2009 sample ($t_{[2]} = 3.81$, $P = 0.003$), and the June 2009 sample differed from the September 2009 sample ($t_{[2]} = -0.08$, $P = 0.05$). This indicates a reduction in population density across both treatments after the June 2008 sampling period.

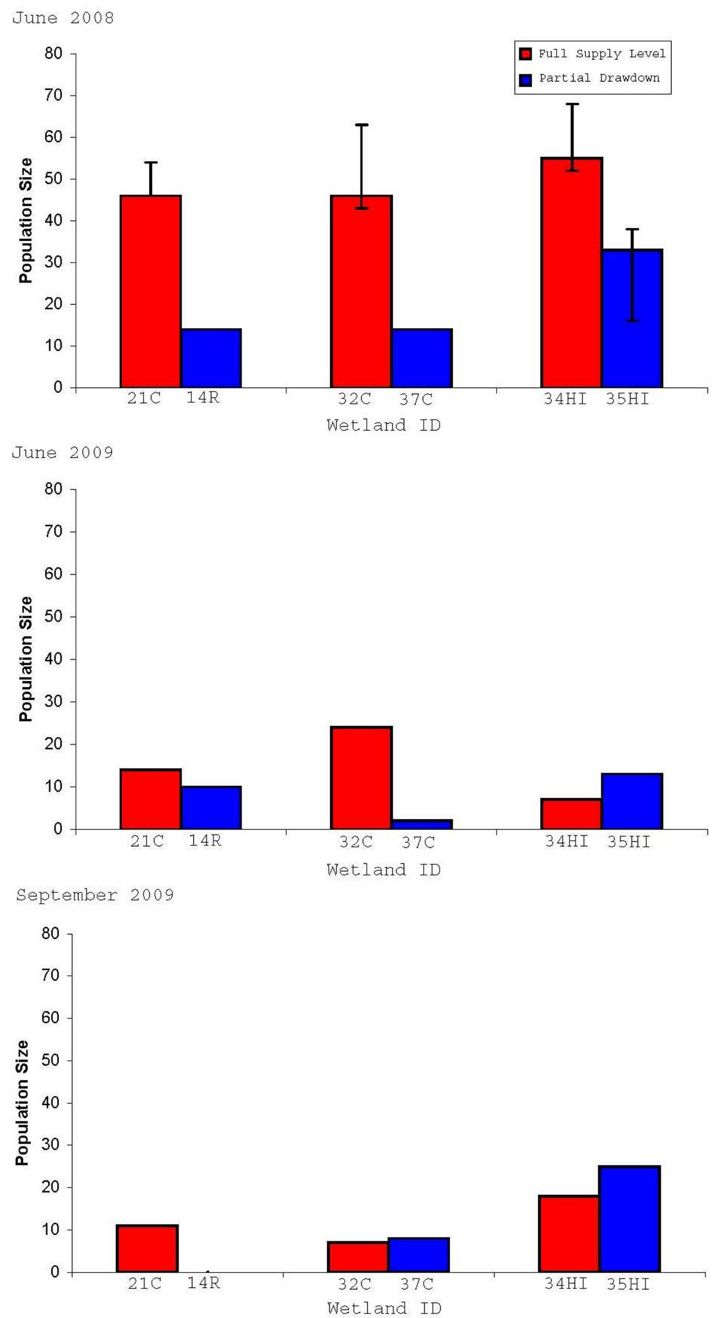


Fig. 6- Population estimates ($\hat{N}$) of muskrats (*Ondatra zibethicus*) , and estimated 95% confidence intervals of $\hat{N}$ (bars without whiskers are M_{t+1}), in each experimental wetland in June 2008, June 2009, and September 2009 at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

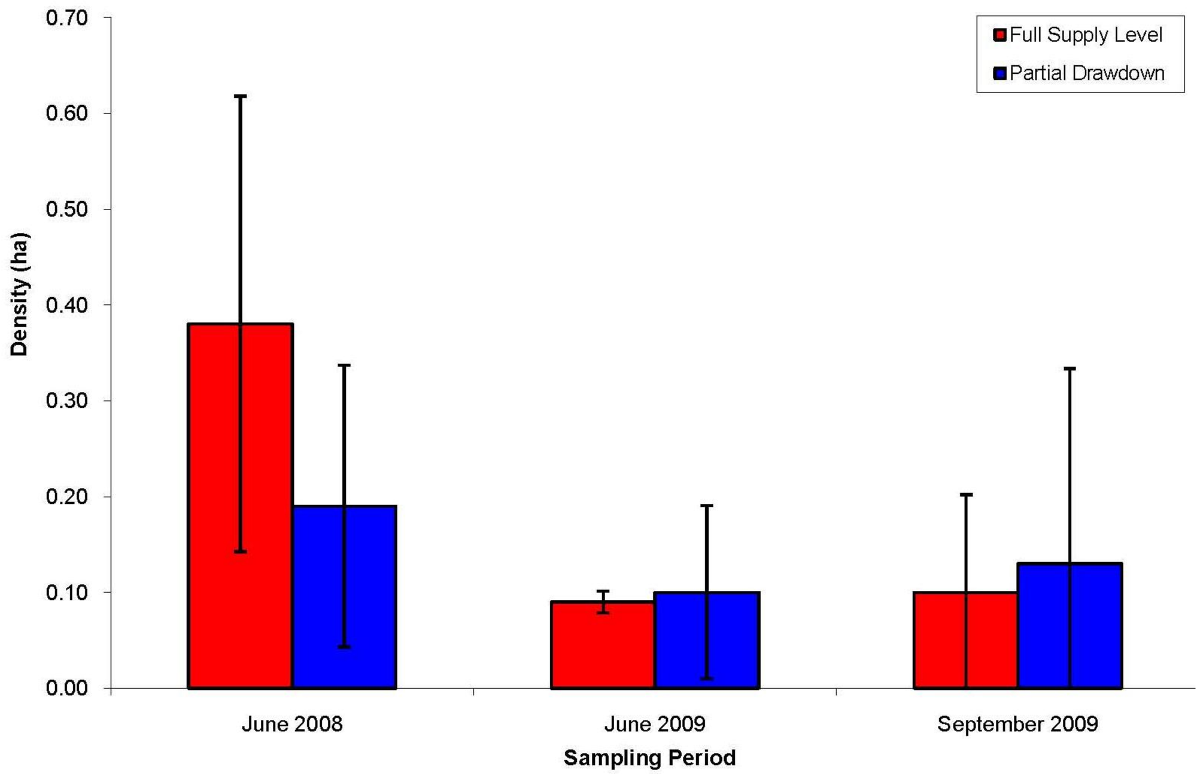


Fig. 7- Average naïve population density estimates of muskrats (*Ondatra zibethicus*), and 95% confidence intervals, in full supply level and drawdown wetlands in June 2008, June 2009, and September 2009 at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

Table 2: Population estimates ($\hat{N}$) of muskrats (*Ondatra zibethicus*) and density per hectare (D/ha) from June 2008 - September 2009 at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

			Full Supply Level		Partial Drawdown			Least Square Means	
Sampling Period			$\bar{x}$	**SE**	$\bar{x}$	**SE**		$\bar{x}$	**SE**
June 2008	$\hat{N}$	*	49.00	3.00	20.33	6.33			
	D/ha		0.38	0.12	0.19	0.08	†	0.31	0.06
June 2009	$\hat{N}$		15.00	4.93	8.33	3.28			
	D/ha		0.09	0.01	0.10	0.05		0.10	0.06
September 2009	$\hat{N}$		12.00	3.21	11.00	7.37			
	D/ha		0.10	0.05	0.13	0.10		0.12	0.06
Least Squares Means			0.19	0.05	0.15	0.05			

*** - denotes levels where arithmetic means were significantly different ($p < 0.05$) between Full Supply Level and Partial Drawdown wetlands**

† - denotes levels where least square means were significantly different ($p < 0.1$) from the September 2009 sample

Recruitment

Histograms of molar indices varied somewhat among years (Fig. 8). To estimate age classes and age ratios I used molar index cut-off values, which apparently differed among years (Erb et al. 1999), of 0.5 for 2008 and 2009, and 0.7 for 2010. Overall mean juvenile to adult female ratio was 5.06 for all years. Pregnancy rate was not well estimated due to small sample sizes, particularly in 2009 and 2010. The number of placental scars counted per pregnant female ranged from 2-15 (Table 3).

The estimated onset of breeding was 20 March 2008 and 18 April 2009. The earliest estimated birth date for both years was 18 April, and the latest 9 August (Fig. 9). Although the data are sparse, frequency histograms of birth dates for FSL and PD wetlands appear similar. No muskrats were caught in 2009 born in Litter Period 1 (22 April through 14 May). The peaks of litter periods two (15 May through 30 June) and three (1 July through 30 July) were similar for both years. I caught one muskrat in 2009 with an estimated birth date of 9 August, representing a possible fourth litter period.

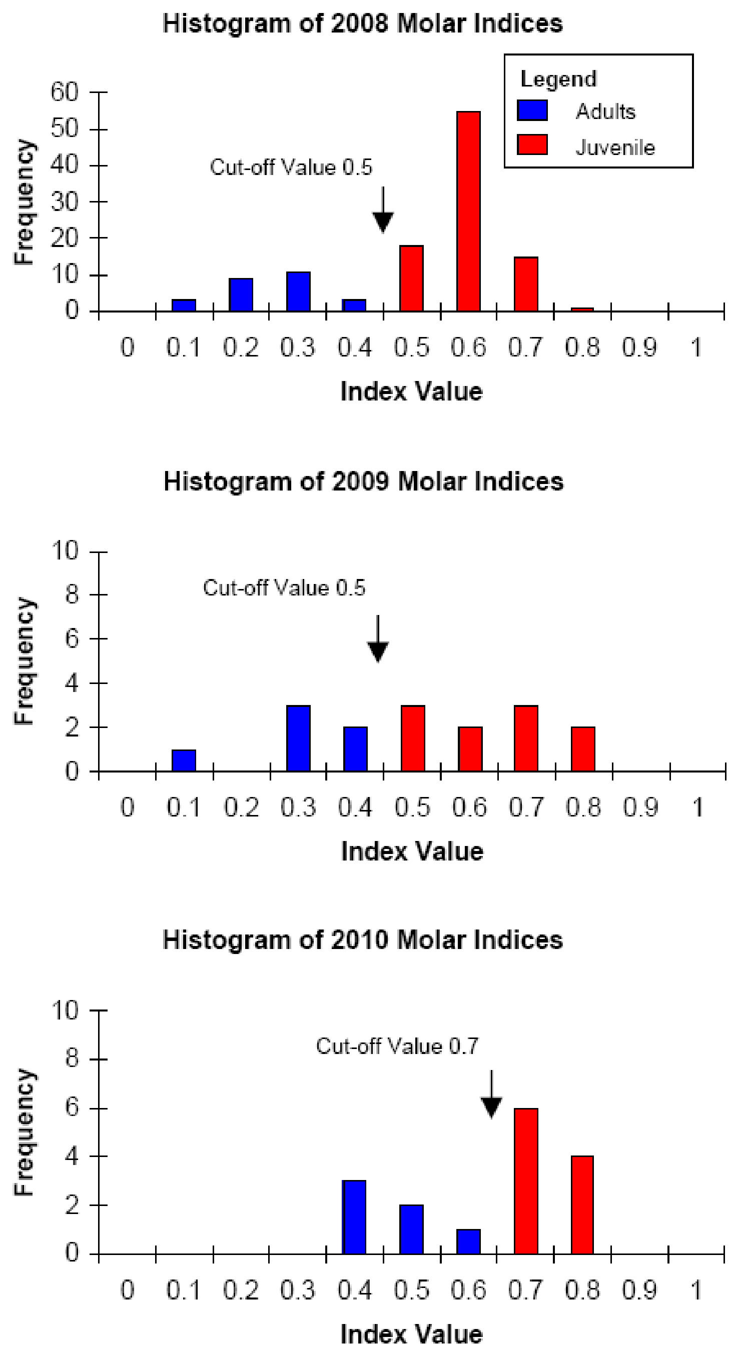
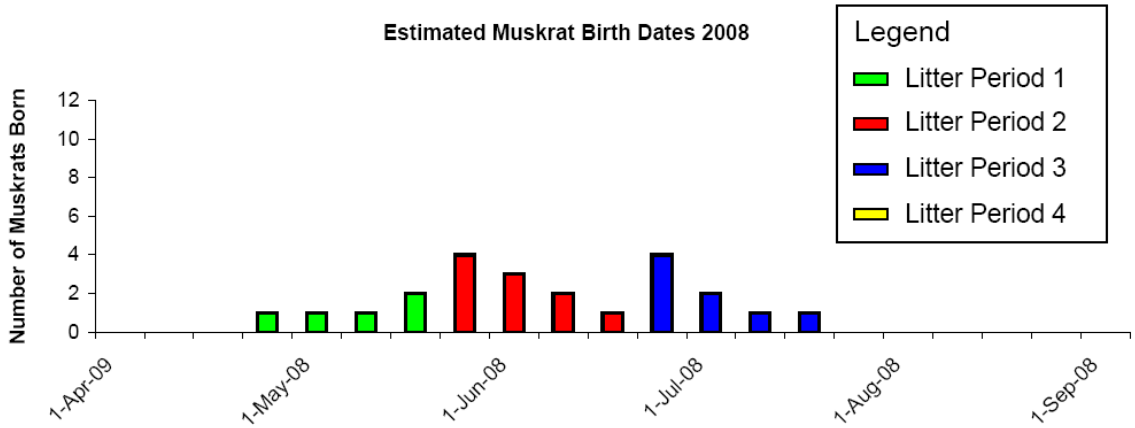


Fig. 8. Frequency of muskrat (*Ondatra zibethicus*) age classes estimated using molar fluting indices as outlined in Erb et al. 1999. Carcasses were collected by local trappers during the legal harvest season (October-May) in 2008 (n =115), 2009 (n =19), and 2010 (n =16) from the Saskatchewan River Delta, The Pas, Manitoba, Canada.

Table 3: Age ratios and pregnancy rates calculated by muskrats (*Ondatra zibethicus*) collected from trappers during legal harvest season October-May 2008, 2009, and 2010 in the Saskatchewan River Delta, The Pas, Manitoba, Canada.

Year	Juveniles	Adult Females	% Juveniles	Juvenile/Adult Female Ratio	Percentage of Adult Females Pregnant	Mean Placental Scars per Pregnant Female
2008	89	13	87.25	6.85	64.70%	7.36
2009	10	4	71.42	3.33	100.00%	9.75
2010	10	2	83.33	5.00	0.00%	0.00



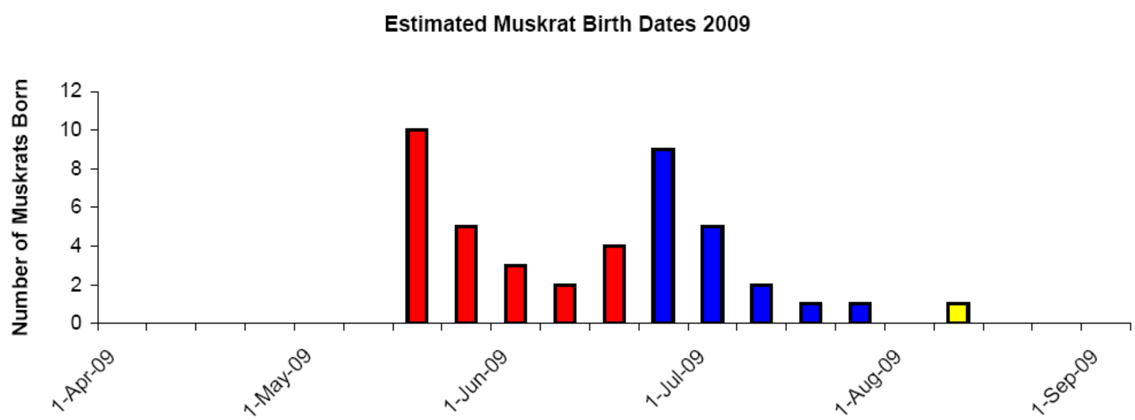


Fig. 9. Histograms of muskrat (*Ondatra zibethicus*) birth dates estimated using body mass regressions of Virgl and Messier (1995) for 2008 and 2009 at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

Body Condition

I calculated 331 BCI's from adult muskrats captured in June 2008 (n = 194), June 2009 (n = 69), and September 2009 (n = 68) sampling periods. Two muskrats were excluded from analysis due to missing attributes for sex. Body condition indices did not differ between treatments ($F_{[1, 319]}$ = 0.80, P = 0.37), or sexes ($F_{[1, 319]}$ = 0.04, P = 0.83), however BCIs differed among ages ($F_{[1, 319]}$ = 505.68, P = 0.0001), and sampling periods ($F_{[2, 319]}$ = 24.69, P = 0.0001) (Table 4). BCIs were higher for adults than juveniles ($t_{[1]}$ = 7.1, P = 0.001). BCIs were lower in the June 2008 sampling period than in September 2009 ($t_{[2]}$ = -2.02, P = 0.001), but were not different in June 2009 than in September 2009 ($t_{[2]}$ = -0.35, P = 0.35).

Table 4: Body Condition Indices of muskrats (*Ondatra zibethicus*) live trapped from the Summerberry Marsh Complex, The Pas, Manitoba, Canada in June and September 2009.

		Full Supply Level			Partial Drawdown			Least Square Means		
Parameter	**Levels**	**n**	$\bar{x}$	**SE**	**n**	$\bar{x}$	**SE**	**n**	$\bar{x}$	**SE**
Sex	**Male** †	144	28.91	0.45	68	27.51	0.66	212	24.60	0.38
	Female	74	27.27	0.88	43	25.91	1.15	117	24.50	0.38
Age	**Adult**	186	30.18	0.30	81	29.90	0.45	267 ‡	31.64	0.32
	Juvenile	32	17.70	0.91	30	18.77	0.94	62	17.46	0.52
Sampling Period	**June 2008**	138	27.84	0.50	56	27.93	0.78	194 ‡	22.53	0.42
	June 2009 *	44	31.72	0.94	24	27.93	1.27	68	24.19	0.58
	September 2009	36	26.20	1.09	31	24.22	1.18	67	26.92	0.50
Least Squares Means		218	24.33	0.33	111	24.76	0.41			

*** - denotes levels where arithmetic means were significantly different ($p < 0.05$) between Full Supply Level and Partial Drawdown wetlands**

† - denotes levels where arithmetic means were significantly different ($p < 0.1$) between Full Supply Level and Partial Drawdown wetlands

‡ - denotes levels where least square means were significantly different ($p < 0.05$)

Mean hematocrit was 0.57 (SE = 0.005) and ranged from 0.44 - 0.71, n = 107. In the ANOVA model containing parameters for water level treatment, sampling period, sex, and age no statistical differences were detected among model parameters (Table 5).

Table 5: Hematocrits of muskrats (Ondatra zibethicus) live trapped from the Summerberry Marsh Complex, The Pas, Manitoba, Canada in June and September 2009.

		Full Supply Level			Partial Drawdown			Least Square Means		
Parameter	**Level**	**n**	$\bar{x}$	**SE**	**n**	$\bar{x}$	**SE**	**n**	$\bar{x}$	**SE**
Sex	**Male**	30	0.55	0.01	19	0.57	0.01	49	0.57	0.01
	Female	32	0.57	0.01	23	0.58	0.01	55	0.58	0.01
Age	**Adult**	47	0.56	0.01	26	0.56	0.01	73	0.56	0.01
	Juvenile	15	0.57	0.01	16	0.59	0.01	31	0.59	0.01
Sampling Period	**June**	32	0.57	0.01	17	0.57	0.01	49	0.58	0.01
	September	30	0.56	0.01	25	0.57	0.01	55	0.56	0.01
Least Squares Means		62	0.57	0.01	42	0.58	0.01			

I calculated 110 N/L quotients from muskrats caught in June 2009 and September 2009 sampling periods. Mean neutrophil count per slide was 55.99 (SE = 1.58), ranging from 16 - 90. N/L quotients ranged from 0.19 – 9.77. In independent counts by two observers of the same fields of view on 12% of our blood slides I found no differences in the number of lymphocytes ($F_{[1, 24]} = 0.06$, $P = 0.81$) or neutrophils ($F_{[1, 24]} = 0.001$, $P = 0.98$) counted by each observer, indicating no observer bias. N/L quotients did not differ between sexes ($F_{[1, 96]} = 0.04$, $P = 0.85$). N/L quotients did differ, however, between treatments ($F_{[1, 96]} = 8.21$, $P = 0.005$) and sampling periods ($F_{[1, 96]} = 4.98$, $P = 0.028$), and age ($F_{[1, 96]} = 4.20$, $P = 0.04$) (Table 6).

Muskrats in FSL wetlands had lower N/L quotients ($t_{[1]} = -0.82$, $P = 0.005$) indicating muskrats in FSL wetlands were less physiologically stressed, than those in PD wetlands. N/L quotients from muskrats sampled in September were lower than June sampled muskrats ($t_{[1]} = -0.5$, $P = 0.028$) indicating that muskrats were more stressed in the June sampling period. Adult muskrats had higher N/L quotients than juveniles ($t_{[1]} = 0.49$, $P = 0.04$) indicating adults were slightly more stressed than juveniles.

Table 6: Neutrophil to lymphocyte quotients of muskrats (*Ondatra zibethicus*) live trapped from the Summerberry Marsh Complex, The Pas, Manitoba, Canada in June and September 2009.

		Full Supply Level			Partial Drawdown			Least Square Means		
Parameter	**Levels**	**n**	$\bar{x}$	**SE**	**n**	$\bar{x}$	**SE**	**n**	$\bar{x}$	**SE**
Sex	**Male**	32	2.12	0.36	20	2.70	0.46	52	1.93	0.36
	Female †	34	1.58	0.31	22	2.51	0.38	56	1.99	0.36
Age	**Adult** *	50	2.14	0.29	26	3.47	0.40	76 ‡	2.46	0.32
	Juvenile	16	0.92	0.17	16	1.19	0.17	32	1.46	0.44
Sampling Period	**June** *	36	2.50	0.34	17	3.92	0.49	53 ‡	2.46	0.39
	September †	30	1.06	0.24	25	1.71	0.26	55	1.46	0.36
Least Squares Means		66 ‡	1.14	0.47	42	2.77	0.35			

*** - denotes levels where arithmetic means were significantly different ($p < 0.05$) between Full Supply Level and Partial Drawdown wetlands**

† - denotes levels where arithmetic means were significantly different ($p < 0.1$) between Full Supply Level and Partial Drawdown wetlands

‡ - denotes levels where least square means were significantly different ($p < 0.05$)

Discussion

House Counts

Partial drawdowns negatively affected the density of active muskrat houses in SMC wetlands during the first year following the partial drawdown. However, the partial drawdowns left refugia in deeper portions of the PD wetlands, in ditches near control structures, and near beaver houses. These areas supported residual muskrat populations at densities similar to those found in full supply level wetlands, as revealed in the analysis of the mark-recapture data. Although the actual population densities were similar among FSL and PD wetlands, muskrats in PD wetlands apparently did not build houses at a similar rate as in FSL wetlands, explaining why we detected a difference in house density, but not in population density. Instead of building houses I speculate that muskrats in PD wetlands occupied beaver lodges, and potentially bank burrows in ditches near control structures, though habitat for bank burrows was minimal. Most of the muskrats I captured in PD wetland were either in traps set on beaver lodges or on runs in ditches near the control structures. Muskrats did not build houses in the central portions of PD wetlands because most of the habitat remaining flooded was open water in wetlands 35HI and 14R, or *Scirpus* in 37C, both of which are habitat types that tend to be selected less than they are available in SMC wetlands (Ervin 2011). Muskrat tend to avoid building houses in open water due to increased wave action or lack of vegetation to anchor houses (Errington 1963).

The density of muskrat houses dropped in FSL wetlands after the June 2009 sampling period to densities similar to those found in PD wetlands. Water depth, winter temperature, and snow depth are often cited as environmental factors affecting overwinter survival (Errington 1963, Clark and Kroeker 1993, Messier et al. 1990, Virgl and Messier 2000, Toner et al. 2010). If overwinter temperatures are low with little snow depth, ice may freeze to the substrate thereby increasing mortality. Typical average mean temperature from October through April at The Pas, MB from 1971-2000 was -9.53 °C and the mean snow depth from the same time frame was 18.71 cm. The overwinter conditions in 2009 were slightly more harsh, but not significantly so, with a mean monthly temperature from October to April of -9.83 °C and mean snow depth from April through October of 16.83 cm (Environment Canada 2010). To mitigate the effects to the substrate managers often 'top-up' water levels to provide deeper water to prevent freezing to the substrate. Nevertheless, if the reduction in number of houses after June 2009 in FSL wetlands was caused by somewhat harsh overwinter conditions this observation suggests that holding water levels at FSL did not mitigate their negative affects on muskrat house density.

Another factor which may have caused the decline in both house and population density in both FSL wetlands could be a relic of the over-bank flood of the Saskatchewan River in 2005. All six of the study wetlands were below FSL prior to the flood event in 2005 (see Appendix A, Figs 1-6), effectively acting like a partial drawdown. The flood event in 2005 acted as a refill, flooding habitat that was dry prior to 2005. Upon reflooding rapid invasion of new habitat is typical, and muskrat populations appear to reach peak population levels 3-5 years following reflooding (Kroll and Meeks 1985, Clark and Kroeker 1993, Clark 2000, Ervin 2011). Data from DUC Canada aerial house counts from 2006-2010 show that house densities were highest in the study wetlands during 2006 and decreased steadily through 2009. Therefore the drop in density in FSL wetlands could have been due to the natural tendency of muskrat populations to decline following the flood five years prior (Clark 2000, Ervin 2011).

Population Estimates

The reduction in abundance in PD wetlands in the June 2008 sample reflects the reduction in the amount of usable habitat. The data indicate that partial drawdowns will support residual muskrat populations during the years of a drawdown. Complete drawdowns often eliminate local muskrat populations during the years of a dry marsh (Errington 1961, Clark 2000), therefore the partial drawdown treatment offers an advantage if mangers want to keep usable habitat to support muskrat populations during the years of a drawdown. Since densities between PD and FSL wetlands were not different, this suggests that the residual flooded habitat in PD wetlands was capable of supporting densities similar to FSL habitat. Furthermore, Ervin (2011) shows that the magnitude of increase of muskrat house densities did not differ between wetlands partially drawndown or completely drawndown in the SRD between 1980 and 1990, providing additional support for this assumption.

Although PD wetlands supported muskrat populations at similar densities as in FSL wetlands, both are below densities reported by Westworth (1974) from the Peace-Athabaska Delta, and in reports from the prairies (Errington 1963, Proulx and Gilbert 1983, Clay and Clark 1985, Clark and Kroeker 1993, Erb and Perry 2003). The SRD has supported high muskrat populations in the past (McLeod 1948). Harsh winters are typical across the northern range of the muskrat, therefore, it is unlikely that winter conditions are an overriding factor contributing to low densities in the SRD. Instead winter conditions compound the effects of underlying factors, especially poor habitat created by stabilized water levels and prolonged flooding (Murkin et al. 2000a).

Recruitment

Age ratios derived form molar indices should be interpreted with caution. Although the placement of the cut off values for 2008 and 2010 is apparent from the histograms of molar indices (Fig. 8), this method incorrectly classified 6 of 11 pregnant females as juveniles in 2008. Precocial breeding of muskrats is extremely rare (0-5%) (Clark 2000, Erb and Perry 2003), therefore I conclude that the six pregnant females classified by this methods to be errant. There is no way to estimate misclassification rate, although frequency histograms of body weight are very similar to the age histograms. Despite these concerns I used the age classification from the molar indices classification method to calculate juvenile to adult female ratios.

Westworth (1974) reported juvenile to adult female age ratios of spring harvested muskrats from the Peace-Athabaska Delta averaged over 1971 and 1972 sampling periods of 9.5:1. Stevens (1953) reported 4.3 juveniles per adult at the Mackenzie Delta, assuming 50/50 sex ratio of adults, would result in 8.6 juveniles per adult female. Both are higher than my estimate of 5.06:1. Westworth (1974) provides estimates from six studies, five in Canada and one in Wisconsin, USA, of which juvenile: adult female ratio ranged from 6.6:1 to 15.4:1. Mathiak (1966) questioned the validity of using age ratios as a means of comparing productivity due to the large natural variation and the variation in sampling techniques. Nevertheless the ratios we found are below estimates from other northern climates.

Muskrat populations generally have the highest rates of reproduction when densities are low (Beer and Truax 1950, Errington 1961, Clark and Kroeker 1993, Clark 2000). Given the low densities I found, one would expect rates of reproduction to be high, and therefore high juvenile: adult female ratios. The low ratios, variable reproductive rates, and moderate litter sizes suggest that exogenous factors such as poor habitat, and endogenous factors such as poor body condition or physiological stress, are linked to low recruitment rates in SMC wetlands.

Birth dates and litter periods appear to be normal in June 2008, but no juveniles were caught in June 2009 that were born in Litter Period 1 (22 April through 14 May). Temperature is correlated with the onset of breeding (Olsen 1959) however mean temperatures for April (2.9°C), May (8.4°C), and June (15°C) 2009 were not below the average temperatures from The Pas from 1971-2000, and therefore not the causative factor.

Body Condition

Although BCIs are a relatively insensitive measure of condition, lack of difference between FSL wetlands and PD wetlands indicates that the partial drawdown did not affect muskrat body condition. As population densities decreased from June 2008 through September 2009, BCIs increased consistent with an inverse relationship to population density. Although higher body condition should increase an animal's ability to reproduce, reproductive rates did not increase as body condition increased. In general these results are consistent with Clark and Kroeker (1993) who also found BCIs did not differ with water level treatment, and that BCIs and population density are inversely related. Clay and Clark

(1985) and Clark and Kroeker (1993) both concluded that BCIs increased as densities decreased, but reproduction did not increase as BCIs increased. The range of BCIs range in these data is lower and does not overlap the range of BCIs reported by Clark and Kroeker (1993) for May and October collected muskrats of 36.6-41.5. This suggests SMC muskrats weigh less in relation to length, reflecting overall smaller body size in northern locales and potentially indicating reduced body condition.

The range of hematocrits I report in this study is higher than hematocrits of muskrats reported by MacArthur (1984a) and Aleksiuk and Frohlinger (1971), and also those reported by Holleman and Dieterich (1973) of 12 rodent species, including the muskrat. However, since I did not use a hematocrit centrifuge in this study, the mean hematocrit value I report is likely biased high. Posterior testing revealed a reduction in hematocrits between the same blood samples spun in the centrifuge I used in the field, and in a hematocrit centrifuge in the lab, therefore comparisons between this study and others should be interpreted with caution.

I found no detectable difference in hematocrit values between treatments. This suggests that the 30 cm reduction in water level in drawdown wetlands did not cause elevated hematocrits, which would indicate a physiological response to increase oxygen affinity, nor anemia, which would be indicative of physiological stress. I feel these are valid comparison since all sampling within this study followed the same procedures.

Elevated N/L quotients of muskrats in PD wetlands suggests a physiological response to stress occurred in response to a reduction in water level. Potential causative factors of increased stress may be due to movement caused by dewatering, or a reduction in quality or abundance of food due to the increased amount of litter in drawdown wetlands. Muskrats in FSL wetlands built houses and were captured near the outer edges of each basin. In PD wetlands these areas were dewatered by the draw down and muskrats were forced to the central portion of the PD basins. Similar changes in environment have been found to increase N/L quotients in commercially raised piglets which were moved from their maternal pens to unfamiliar pens (Puppe et al. 1997), and also in pigs which were shipped (McGlone et al. 1993). It should be noted that these effects persisted throughout the drawdown after the initial reduction in water levels in the summer of 2007 indicating potential prolonged stress in muskrats in PD wetlands. These results indicate that this management practice may induce physiological stress, which could temporarily affect an individual's ability to survive and reproduce (Servello et al. 2005). The long term benefits of the management practice should, however, surpass any short-term ill affects induced by a drawdown.

I also found N/L quotients of adults to be higher than juveniles. N/L quotients have been reported to increase in humans (Lugada et al. 2004) and dogs (Faldyna et al. 2001) with age, and our results are consistent with that pattern.

Although I found no other examples in the literature of N/L quotients varying among seasons I speculate that this finding is consistent with the finding of MacArthur (1984a) who reported increases in hematocrits in winter. Although he did not relate elevated hematocrits to stress, I speculate that N/L quotients are higher in the spring following the stresses of hypoxia and limited access to food overwinter. It seems logical that when these stressors are eliminated, during the course of the summer with ready access to food, that lower N/L quotients should result in fall, as these data show.

Low muskrat densities, and low recruitment compared to other northern deltas in the SMC are likely due to degenerating wetland habitat conditions created by prolonged water level stabilization. The highest muskrat densities in the SRD, apparent from historical records dating back to the 1930’s (R. Ucthmann, Manitoba Conservation, The Pas, pers. comm., Mcleod 1950) occurred in the decade following the drought of the 1930’s. Upon reflooding of the wetlands by high water levels in the river, and impoundment by newly constructed water control structures, high quality habitat was abundant, and muskrat populations boomed (McLeod 1950). This large scale completion of the wetland cycle was responsible for supporting the largest muskrat populations on record, and has not been mimicked in scale since.

Smaller scale water level manipulation efforts by various managers, most notably Ducks Unlimited Canada, have produced similar increases in muskrat populations, though to a lesser extent (Ervin 2011). Over the years water level management in the SMC has varied but relatively high water and conservative management practices has promoted the current degenerating wetland conditions. Although expensive and logistically difficult, the results presented herein, and in Ervin (2011), suggest that a large scale drawdown and refill would once again support high muskrat populations in the SMC and more generally the entire SRD. Further study on muskrat population response to the reflooding of the PD wetlands is needed to support this speculation.

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CHAPTER 3: MODELING HOUSE SITE SELECTION OF MUSKRATS *(Ondatra zibethicus)* USING LOGISTIC REGRESSION TO CREATE RESOURCE SELECTION FUNCTIONS.

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Abstract

I studied muskrat (*Ondatra zibethicus*) habitat selection in response to a partial (30 cm) late summer drawdown in the Saskatchewan River Delta, Manitoba, Canada, 2007 through 2009. I mapped house locations by conducting surveys along transects from airboats in 2008 and 2009. I classified vegetation from aerial imagery, taken each year in early July, using object oriented segmentation in Definiens eCognition software. I included the vegetation classification and additional habitat covariates to compare active house (used) locations to random (unused) locations using a resource selection function (RSF) derived from Design I sampling. I assessed the nutrient quality of four vegetation types consumed by muskrats for acid detergent fiber (ADF) and crude protein (CP) to link to habitat selection. The partial drawdown resulted in an increase in the amount of senescent vegetation. *Carex spp.* and *Typha spp.* were negatively affected by the fall drawdown, but the amount of open water did not change after two years of the partial drawdown. Muskrats preferred *Typha spp.* among all vegetation types, and selected for the rooted vegetation condition over the

floating vegetation condition. Active house locations were positively correlated with distance to upland and water depth, and negatively correlated with distance to open water and greenness of vegetation index. *Typha spp.* had the lowest ADF content and the highest CP content. The floating and rooted conditions of *Typha spp.* did not differ significantly in ADF or CP. The partial drawdown did not significantly affect ADF or CP in the emergent vegetation species that were sampled.

Introduction

Wetland managers often use muskrat abundance as an indicator of overall wetland health and often base management plans on directly influencing muskrat populations (Murkin et al. 2000). Muskrats are the dominant herbivores in many aquatic ecosystems (Boutin and Birkenholz 1987, Erb and Perry 2003) and are presumed to play an important role in the wetland succession (Weller and Spatcher 1965, Danell 1978, Clark 2000). They consume above and belowground parts of aquatic and terrestrial plants (Perry 1982) as food and in lodge construction. Felling of vegetation and lodge building effects decomposition rates, nitrification rates, invertebrate abundance, plant diversity, and waterfowl use and abundance (Weller and Spatcher 1965, Danell 1977, Godshalk and Wetzel 1978, Connors et al. 2000). Understanding muskrat use of habitat in SMC wetlands undergoing water level management will aid managers in habitat management.

Dwellings, or houses, are centers of activity (Proulx and Gilbert 1983) and offer an obvious sign of habitat selection. Muskrats differentially select habitat based on water depth and emergent vegetation (Proulx and Gilbert 1983, Kroll and Meeks 1985, Clark 2000, Erb and Perry 2003). Selection of vegetation is potentially due to differences in food quality or preference for house building material (Welch 1980, Jelinski 1989, Campbell and MacArthur 1995, 1998). In northern climates water depth at lodges must be deep enough to prevent freezing of the substrate. Vegetation can trap snow and act as an insulator reducing ice thickness and preventing ‘freeze outs’ (Messier et al. 1990, Clark 1994). When ice freezes to the substrate access to rhizomes is restricted and survival is diminished. In prairie wetlands Clark (1994) found that muskrats tended to avoid areas <1 cm deep and the average water depth at lodges was 38 cm. Muskrats tend to avoid deep open water habitats possibly due to increased wave action (Errington 1963); lack of vegetation in close proximity for food and lodge construction, and the inability to anchor houses in deep water (Clark 2000). Conversely, shallow water zones expose them to predation and winter freeze outs (Clark and Kroeker 1993, Clark 2000).

Because distribution and quality of resources may vary over space and time, habitat selection and availability of suitable habitat may vary among populations across spatial and temporal scales (Boyce 2006). Habitat selection by muskrats has been studied extensively in prairie ecosystems, however considerably less is known about muskrat habitat selection in the northern deltaic systems. Differences in water regime, depth tolerances and spatial distribution of wetland plants, and climate may all be factors contributing to differences in habitat selection by muskrats in northern deltaic systems compared to the prairies. Studies have been carried out in the SRD (Mcleod 1948, Phillips 1980) and in the Mackenzie and Peace-Athabaska River deltas respectively (Stevens 1953, Westworth 1974), but new, more sophisticated methods have since been developed to assess habitat selection.

Since hydroelectric developments on the Saskatchewan River in the 1960's have altered river flows and effected over bank flood frequency in the SRD (Fig. 1), wetland managers and resource users have focused on water level management as a means of managing wetland resources. Myriad dykes, ditches, and water control structures have been installed in the SRD to aid in water level control and manipulation in attempts to manage habitat for muskrats and waterfowl. Water level drawdowns were implemented from 1979-1990 in the SMC to enhance habitat, but resulted in excessive and prolonged vegetative growth. When compounded with increasing cost and regulatory difficulties, management was largely abandoned until further study could quantify the effects of water level manipulation on vegetation and water quality (Watchorn 2010), water birds and waterfowl (Baschuk 2010), and muskrats (Ervin 2011). Water has since been impounded in wetlands resulting in the less productive degenerating wetland or lake stages described by van der Valk and Davis (1978) and van der Valk (2000). As a result muskrat populations are low in the SMC, <1/ha (Ervin 2011), compared to other northern deltas (Stevens 1953, Westworth 1974), and considerably lower than densities reported in prairie ecosystems (Errington 1963, Proulx and Gilbert 1983, Clay and Clark 1985, Erb and Perry 2003).

This study focuses specifically on habitat selection of muskrats in response to a water level drawdown. I use multivariate logistic regression to create design I resource selection functions (RSF) (Manly et al. 2002) to assess which habitat variables are most strongly correlated with muskrat habitat selection in SMC wetlands, and how water level manipulation affects habitat selection and food quality. Our intent is to provide wetland managers with an understanding of how muskrats use habitat in the SMC in response to habitat manipulation.

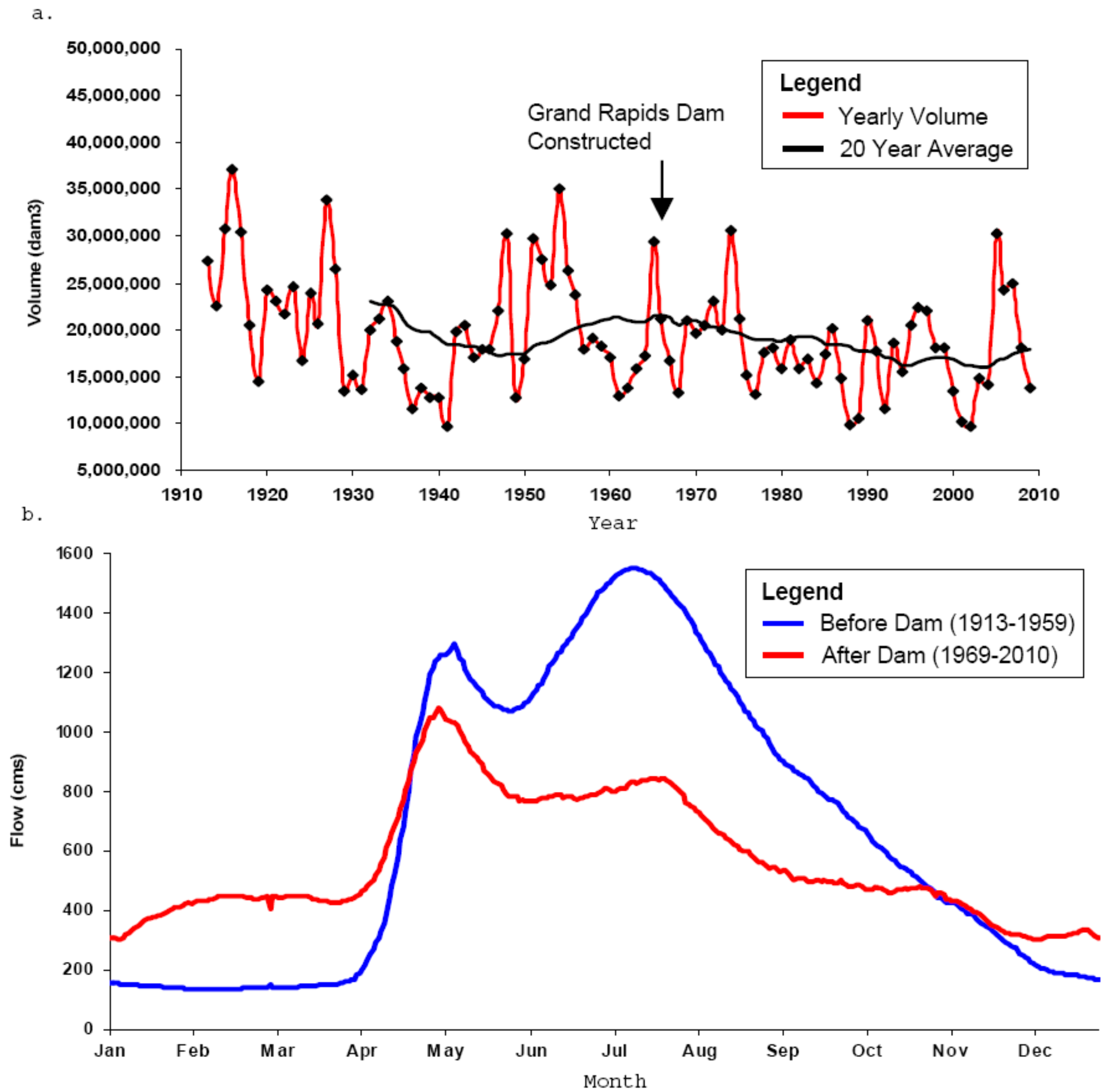

Fig. 1. (a) Total yearly flow of the Saskatchewan River at The Pas, Manitoba, Canada for the past 100 years. (b) Mean weekly flow of the Saskatchewan River at The Pas, Manitoba, Canada before and after the construction of the Grand Rapids Dam in 1968.

Study Area

The SMC is located in the southeastern corner of the SRD, approximately 24 km downstream of The Pas, Manitoba, Canada. The SMC encompasses 14,000 ha, of which approximately 7,000 ha are wetlands downstream from the head of the Summerberry River and extending to the delta at Cedar Lake. Ducks Unlimited Canada (DUC) manages 28 control structures within the SMC, capable of a range of water level manipulation from full supply level to complete drawdown. Control structures in the SMC were built in 1978, and active water level management occurred from 1979-1990. No managed drawdowns have occurred in the SMC since 1990. Annual daily mean temperature at The Pas, Manitoba from 1971-2000 was 0.1°C, and 162 days per year had a snow depth of at least 1cm (Environment Canada, 2010).

The research group selected six study wetlands based on location, size, and ease of access and water level. At the time of study dense emergent vegetation primarily composed of sedges (*Carex spp.*), horsetails (*Equisetum spp.*)¸reed grass (*Phragmites australis*), cattails (*Typha spp.*), and bulrushes (*Scirpus spp.*) dominated the emergent zone of the study wetlands. Open water habitat was present in the deeper central portion of each study wetland, and also interspersed with vegetation toward the periphery of the wetlands. Flooding tolerances, distributions, and growth habitats of emergent macrophytes are apparently different from that of similar species in the prairies. For example, *Phragmites spp.* persists and continues to grow in water that is 1 m deep. *Typha spp.* and *Carex spp.*, among other common emergent macrophytes, grow in floating mats suspended above the substrate. Open water habitat was present in the deeper central portion of each study wetland, and also interspersed with vegetation toward the periphery of the wetlands. The maximum depth recorded in any study wetland was 145cm.

Methods

Water Level Manipulation

Each of the six study wetland has a water control structure to facilitate water level manipulation and control. Water level manipulation began in the spring of 2007. Partial drawdowns, to approximately 30 cm below full supply level (FSL) (i.e. maximum legal water level), were implemented on the three ‘partial drawdown (PD)’ wetlands; 14R, 35HI, and 37C. The remaining three ‘full supply level (FSL)’ wetlands, 21C, 34HI, and 32C, were held at approximately FSL and designated as experimental controls (Fig. 3). Wetlands remained at approximately these levels through 2010 (Appendix A). Water levels were recorded weekly throughout the summer sampling periods, and data loggers recorded winter water levels, to ensure water remained at target levels.

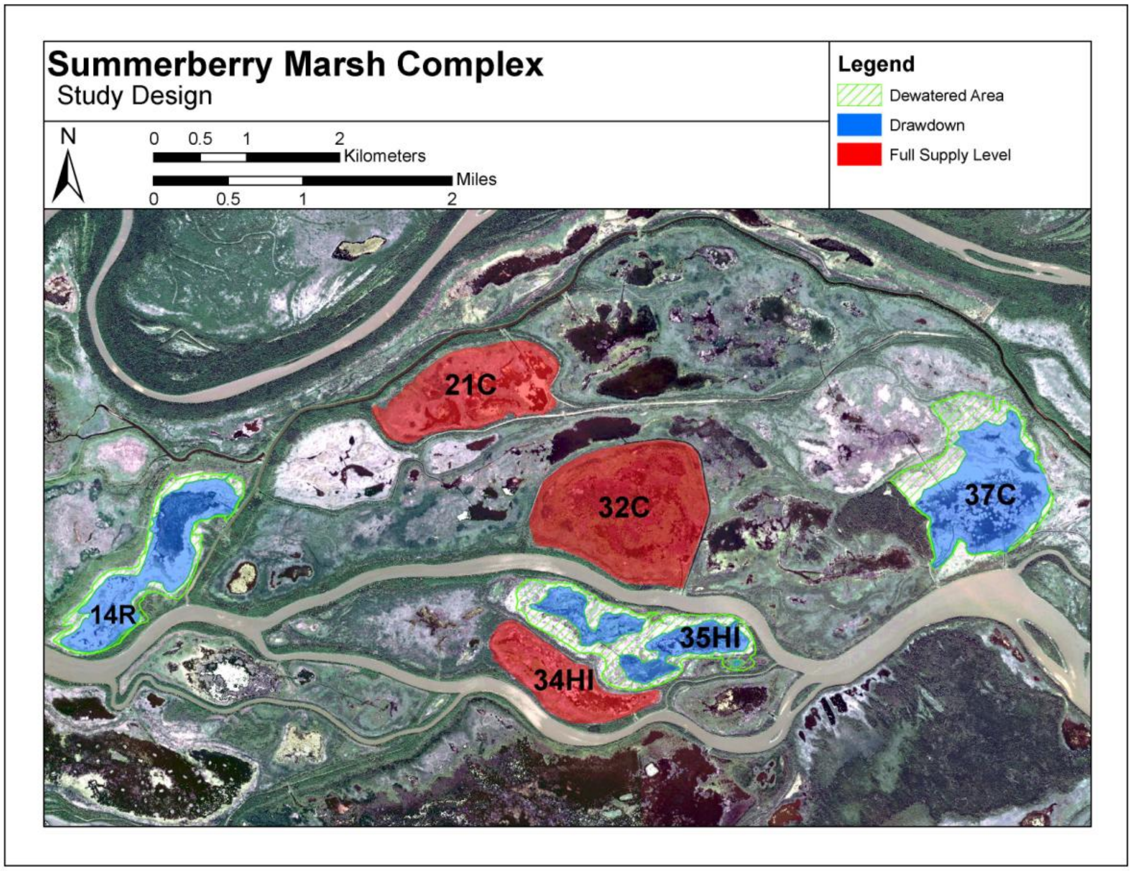

Fig. 2. Study design displaying full supply level and drawdown wetlands, as well as the area dewatered by the partial drawdown, at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

House Counts

I conducted house count surveys from air boats in June 2008, June 2009, September 2009, and June 2010. I conducted surveys on transects that were spaced approximately 40 m apart and covered the entirety of each study wetland (Fig. 3). I stopped the airboat at each house or feeding platform in order to mark the location with a Garmin GPSMap 76c, measure depth to the nearest centimeter, record dominant vegetation, and assess activity. I designated all muskrat structures that were conical in shape and constructed of cut emergent vegetation as houses. I designated an object as a feeding platform if it had a flat upper surface and was constructed of emergent vegetation. Although I did not measure the height of each house, houses were generally taller (i.e. 30-150 cm above water surface) than feeding platforms (i.e. 5-10 cm above water surface). Houses and feeding platforms were designated as active in spring surveys if they appeared to be built the previous fall (i.e. houses 60-150 cm above water surface), or in surveys after green up if freshly cut, green vegetation was present. Additional areas of activity, such as muskrat runs, beaver houses, beaver slides, etc, were marked for use in trap site selection, but not recorded as houses or feeding platforms. For analysis purposes I considered house count surveys to be a census of all muskrat houses present during each sampling period.

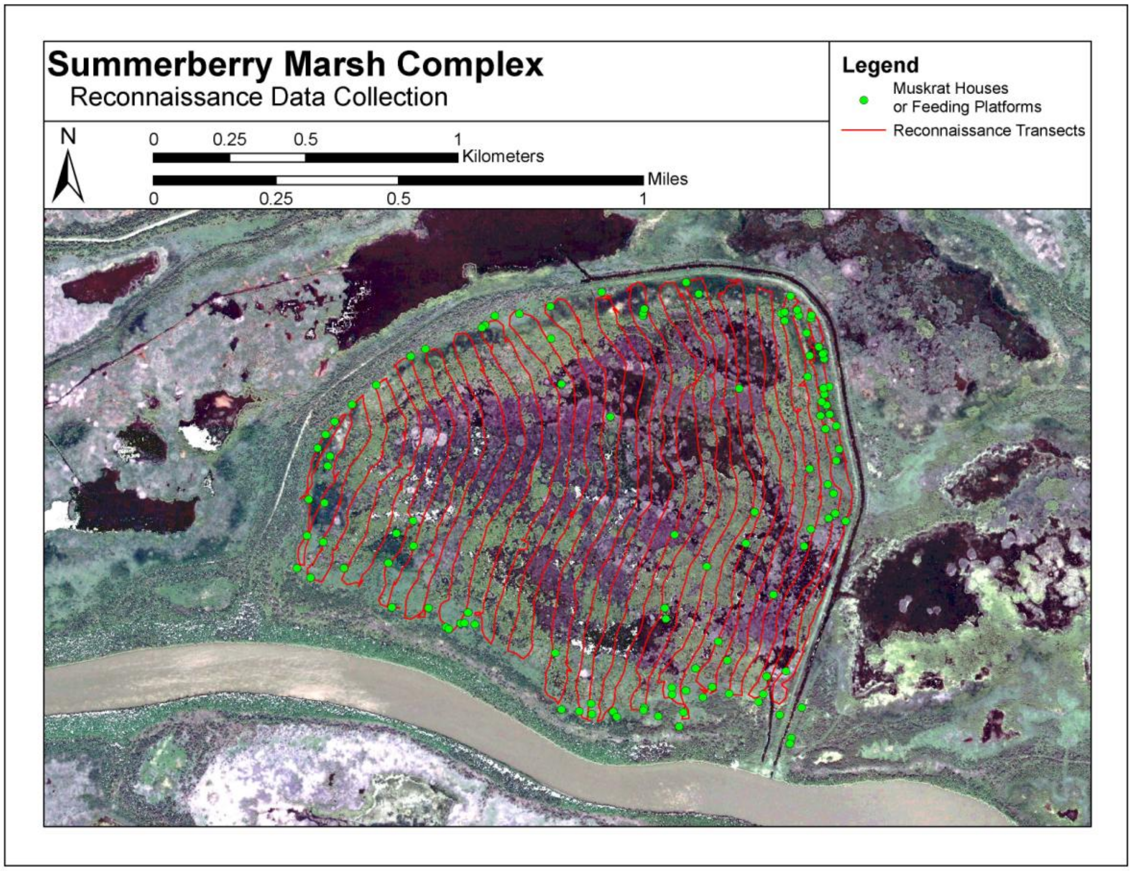

Fig. 3. Survey carried out in wetland 32C prior to mark-recapture sampling on 23 June 2009 to locate muskrat (*Ondatra zibethicus*) houses at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

Vegetation Mapping

I censused emergent vegetation within the study wetlands from 60 cm resolution Quick Bird aerial imagery in a geographic information system (GIS). True color and near Infrared images were taken during the first week of July in 2007-10. The first step in image classification was to collect ground truthing points along transects spaced approximately 50 m apart at 50 m intervals (Fig. 4). I recorded either the dominant vegetation type or if no vegetation was present, I recorded an attribute for ‘open water’ at each point. Then I segmented the images into polygons using Definiens eCognition software (Trimble Navigation Limited 2010, Sunnydale CA, USA) and used the ground truthing points to attribute a portion of the segmented polygons. I then used the polygons containing a ground truthing point as response variables in logistic regression (the reference category was water) to predict the vegetation class of each polygon. I classified the segmented polygons using PROC LOGISTIC in SAS (SAS Institute Inc. Cary, NC, USA) into eight categorical vegetation classes (*Carex spp.*, *Equisetum spp.*, *Phragmites spp.*, *Scirpus spp.*, *Typha spp.*, trees, senescent vegetation, and open water) using the spectral signatures of each polygon.

I selected models based on prediction accuracy as the primary criteria, and AIC as secondary criteria. I calculated prediction accuracy using two methods. I calculated prediction accuracy by first calculating an individual percent accuracy (the number of polygons, which contained a ground truthing point that was correctly predicted, divided by the total number of polygons containing ground truthing points) for each vegetation class. Average prediction accuracy (%) was calculated by summing the individual percentages of each vegetation class. I calculated a second measure of prediction accuracy, % of polygons predicted correctly, by calculating the percentage of polygons which contained a ground truthing point that were correctly predicted by the logistic regression models. Tables 1-4 Appendix B provide detailed results of model predictions.

I used the model predictions from the model with the highest prediction accuracy to attribute each polygon with a ground cover class in ESRI ArcMap 9.2.

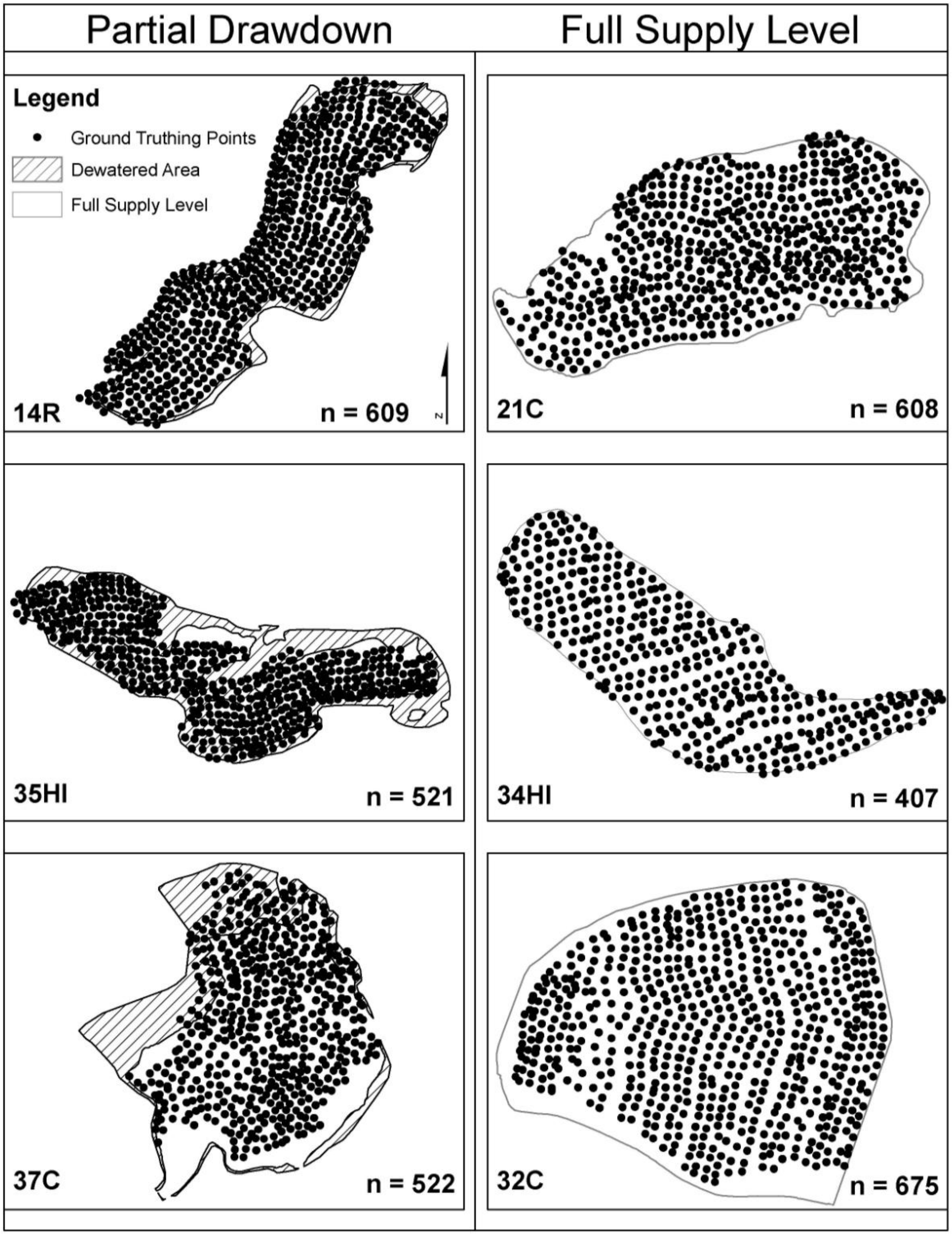

Fig. 4. Ground truthing points collected from 5-13 July 2009 in six wetlands at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

Habitat Condition

For this study, I define three categorical ‘habitat conditions’ as the differences in condition between the same species of (1) rooted emergent vegetation and (2) floating emergent vegetation, or (3) open water. I use the same points collected for ground truthing to create GIS shapefiles delineating habitat conditions. I attributed each ground truthing point with a habitat condition at the time of collection. I used these points to create Thiessen polygons in ESRI ArcToolbox (Environmental Systems Institute, Redlands, CA, USA). Then I used the spatial join tool to attribute each polygon with the habitat condition of the point from which it was created. The result was a polygon shapefile covering the entirety of each wetland with each polygon containing an attribute for habitat condition (Fig. 5).

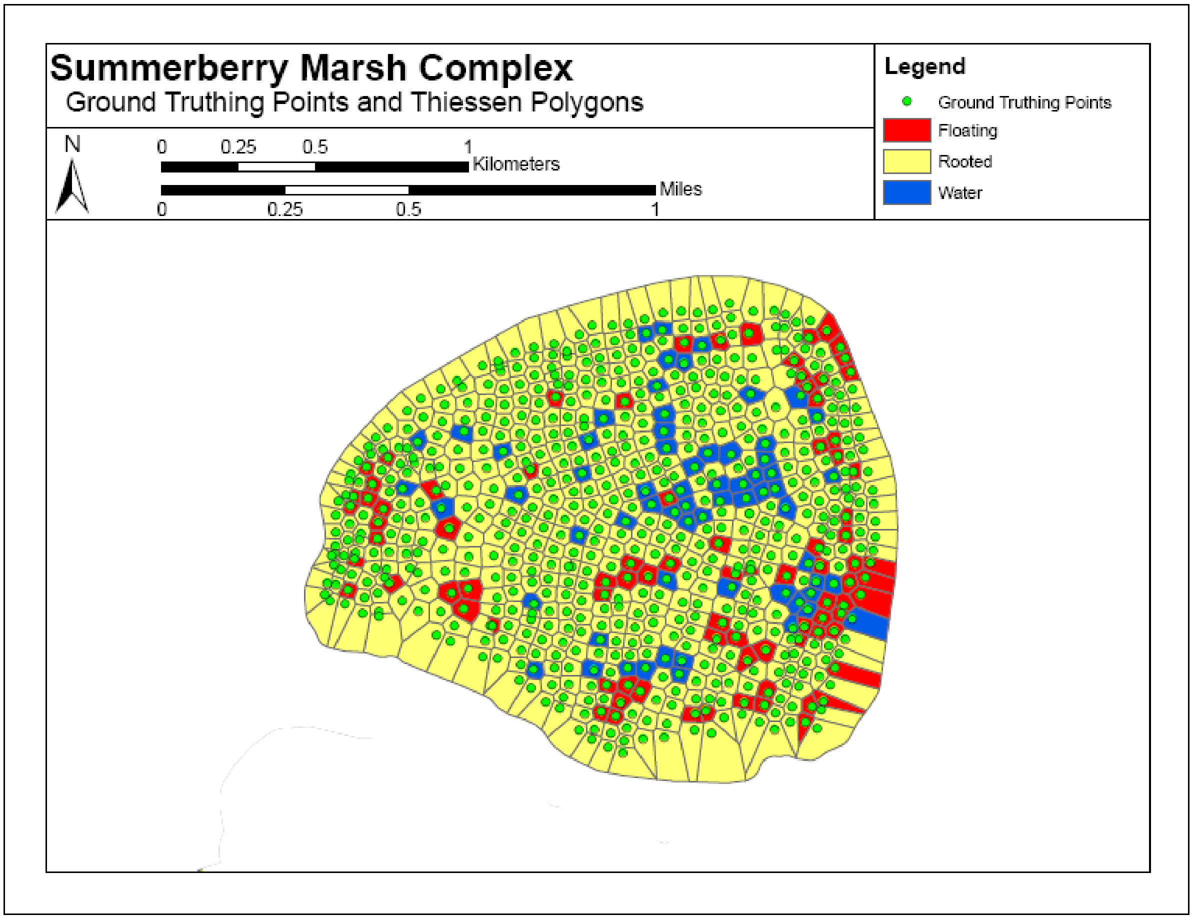

Fig. 5. Ground truthing points used to create Thiessen polygons to delineate habitat types in wetland 32c in the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

I then used the identity tool in ArcToolbox to combine the attributes and geometry of the ground cover shapefile with the habitat type shapefile. Since the vegetation classification was a census of all available space, and the habitat condition shapefile was derived by extrapolating point data to polygon data (using Thiessen polygons), I assumed the habitat condition attribute to be less accurate and in need of correction. I corrected the habitat condition attribute by following these rules. (1) If the vegetation classification of a polygon was predicted by the logistic regression model as water, then the habitat condition attribute was corrected to water. If the habitat condition attribute was water, but the vegetation classification was predicted as anything other than water, then (2) any polygon that touched the boundary of a polygon correctly attributed as rooted was given a habitat condition attribute of rooted. And likewise any polygon that touched the boundary of a polygon correctly attributed as floating was given a habitat condition attribute of floating. In cases where a polygon touched both a rooted and a floating polygon, habitat condition was changed to rooted. This provides a conservative estimate of the amount of floating vegetation in each wetland.

Habitat Condition*Vegetation

I tested how the interaction of habitat condition (i.e. rooted or floating) and vegetation type affected muskrat habitat selection. I merged the habitat condition and vegetation type data columns into one data column with 13 unique values. I built two groups of models one with both vegetation type and habitat condition separate as main effects, and another with cover and habitat condition combined as one main effect.

Depth

Each ground truthing point also contains an attribute for water depth. I used these points to create triangulated irregular network (TIN) surfaces for the study wetlands in ArcMap 3d Analyst. Then I converted TINs to 30 cm grid cell size raster surfaces containing a continuous attribute for depth. I then attributed each muskrat house and random point with water depth using the Spatial Join tool in ArcMap. Water levels, recorded weekly in the summer and continuously by data loggers in the winter, were sufficiently static in the study wetlands throughout the project to use these water surfaces for all analyses.

Additional Covariates

I considered distance to open water, distance to upland, distance to trees, normalized vegetation index (NDVI), and a vegetation robustness index, 'greenness' as additional continuous covariates in the RSF. I calculated distance to open water, distance to upland, and distance to trees using the Near tool in Arc Toolbox. I measured distance to open water as the shortest distance to a polygon classified as water. I measured distance to upland as the nearest distance to water depth of 0 cm. I measured distance to trees as the shortest distance to a polygon classified as trees. I calculated NDVI for each ground cover polygon using the following formula:

$$NDVI = \frac{(mean\_NIR - mean\_red)}{(mean\_NIR + mean\_red)} \quad [1]$$

Then I used NDVI values to calculate a vegetation robustness index, which I arbitrarily named 'greenness'. I subtracted the mean NDVI value from the NDVI value of each segmented polygon and multiplied by a coefficient to scale all values between -1 and 1 so that water had the lowest index value of -1 and the polygons with the highest NDVI values had a value of 1. This scaling should ensure that the values are comparable across years regardless of the time of green-up.

I considered two additional categorical covariates in the RSF. I added a covariate, ‘treatment’, to designate whether a marked house or random location was in an FSL or PD wetland. Additionally I created ‘sampling period’ covariate to designate in which sampling period each observation occurred.

I created a set of random points equal to the number of marked houses, stratified by ‘treatment’ and ‘sampling period’, using Hawth’s tools Generate Random Points tool (Beyer 2007). Random points represent available, unused habitat. I added an attribute called ‘response’ to designate each point as a marked house (1) or a random location (0), and then merged the shapefiles into one. I then added attributes for all of the covariates to be included in the logistic regression to the point shapefiles of marked house and random points. Vegetation type, habitat condition, NDVI, greenness, distance to open water, distance to upland, and distance to trees were added using the spatial join tool in ArcMap. I added the depth attribute to the point shapefiles using Hawth’s Tools raster intersect tool.

Statistical Analyses

I used these covariates to create a Design I RSF (Manly et al. 2002) using SAS Proc Logistic (SAS Institute Inc. Cary, NC, USA). Before building models I performed univariate tests on continuous covariates using Student’s t-tests, and categorical covariates using Fishers exact tests in JMP 8.0 to compare how the covariates differed between marked houses and random locations, and also between marked houses in FSL and PD wetlands. I tested all continuous covariates for correlation in JMP and removed the least significant of the pair of correlated variables if $r > 0.70$. I tested continuous variables for normality and performed square root transformations where necessary. I considered interaction terms for all continuous habitat variables.

Initially, I created models containing only one covariate + intercept to determine how individual covariates ranked in terms of explaining variation in the data. I then built models containing all habitat covariates as main effects, as well as models with all covariates as main effects and all interactions. I built reduced models using stepwise selection (SLENTRY α = 0.1), and built additional models with fewer parameters using habitat variables of particular interest given the biology of the muskrat. I then compared models using Akaike's Information Criterion (AIC) (Burnham and Anderson 2002). I also calculated deviance, pseudo-R^2, model weight, and percent concordance as additional indicators of model performance. I made final model selections after considering AIC values.

Nutritional Analysis of Vegetation

I conducted nutritional analysis of vegetation on four vegetation types (rooted *Typha spp.*, floating *Typha spp.*, *Phragmites spp.*, and *Carex spp.*) that are known to be consumed by muskrats. I selected these three species bases on the relative proportion of houses in these vegetation types found during house count surveys. I collected all samples between 20 September and 26 September, 2009. I gathered stems and rhizomes from five samples of each type from the 25th and 75th depth quartiles in each wetland for a total of twenty samples per vegetation type in each wetland. I weighed all samples upon collection and froze them until further processing. All samples were dried, ground, and analyzed at Dairyland Labs Arcadia, Wisconsin, USA.

Each sample was analyzed for Kjedahl-N (AOAC 2000) and acid detergent fiber (ADF) (AOAC 1996). Kjedahl-N was converted to crude protein (%) by multiplying by 6.25 (AOAC 2000). I followed the procedures outlined by Campbell and MacArthur (1998) using an ANOVA to test for differences in nutritional content between the four vegetation types and between the water level treatments. I also used one sided t-tests to test for effects of treatment and plant part on both ADF and CP.

Results

House Counts

I marked 443 active muskrat houses between all sampling periods. I only used active houses in analysis and excluded inactive houses since they were not inhabited by muskrats at the time of study.

Vegetation Mapping

Among all wetlands I collected a total of 3342 ground truthing points for use in attributing segmented polygons (Fig. 5). The distributions of emergent macrophytes as a function of depth was similar between FSL and PD wetlands given the 30cm managed water level reduction (Table 1). The partial drawdown apparently resulted in an increased amount of senescent vegetation in PD wetlands in 2008 and 2009 (white areas in Figs. 6) compared to FSL wetlands (Figs. 7).

Table 1: Mean and standard error (SE) water depth (cm) in different vegetation types in full supply level (FSL) and partial drawdown (PD) wetlands at the Summerberry Marsh Complex, The Pas, Manitoba, Canada July 2009.

	FSL			**PD**		
Vegetation Type	**n**	**Mean (cm)**	**SE**	**n**	**Mean (cm)**	**SE**
Carex	327	37.95	1.17	416	10.61	0.73
Equisetum	147	39.67	1.74	68	22.53	1.79
Phragmites	554	75.73	0.90	292	29.97	0.87
Typha	236	78.06	1.37	403	35.96	0.74
Water	258	87.77	1.31	263	54.42	0.91
Scirpus	159	92.82	1.67	160	51.74	1.17

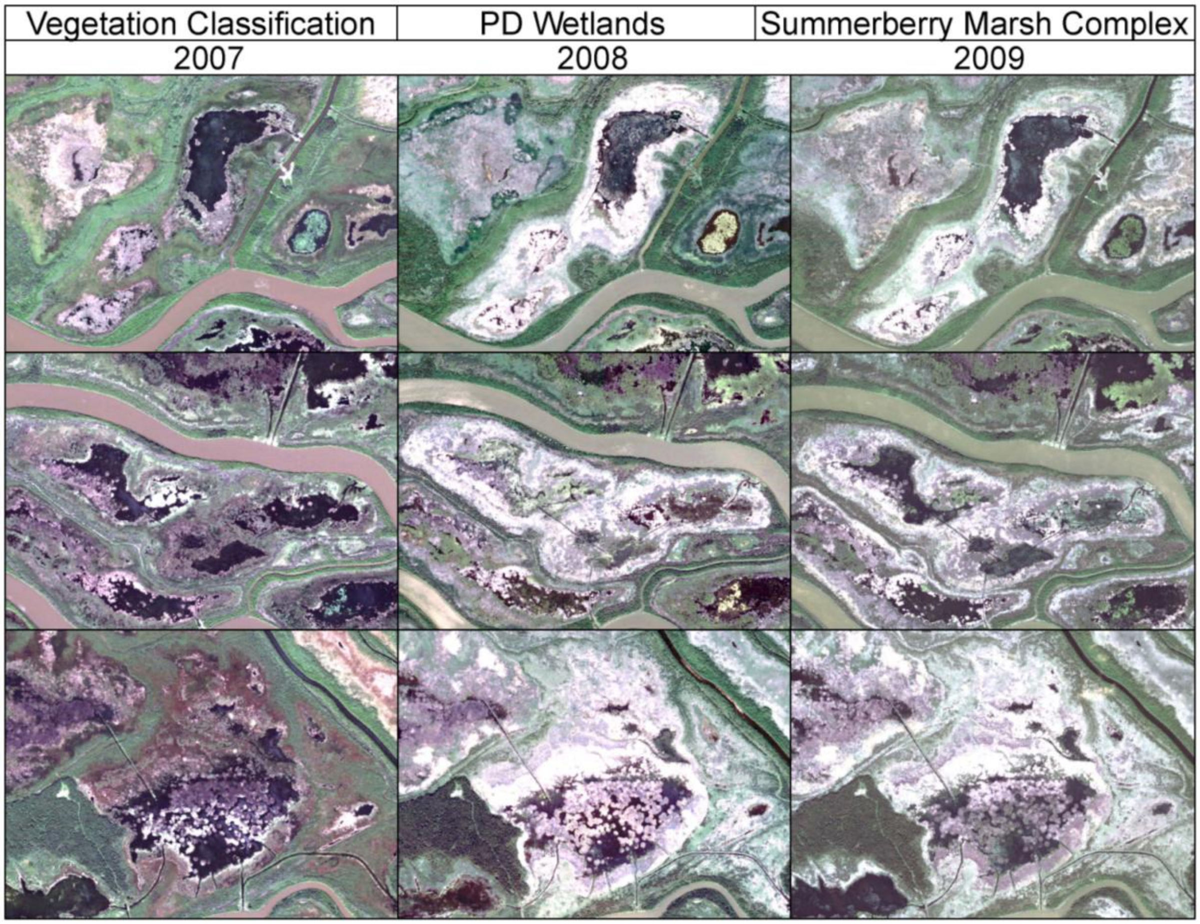

Fig. 6. Quickbird® imagery of partial drawdown (PD) wetlands in 2007 (pre-drawdown), and 2008 and 2009 (post-drawdown) at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

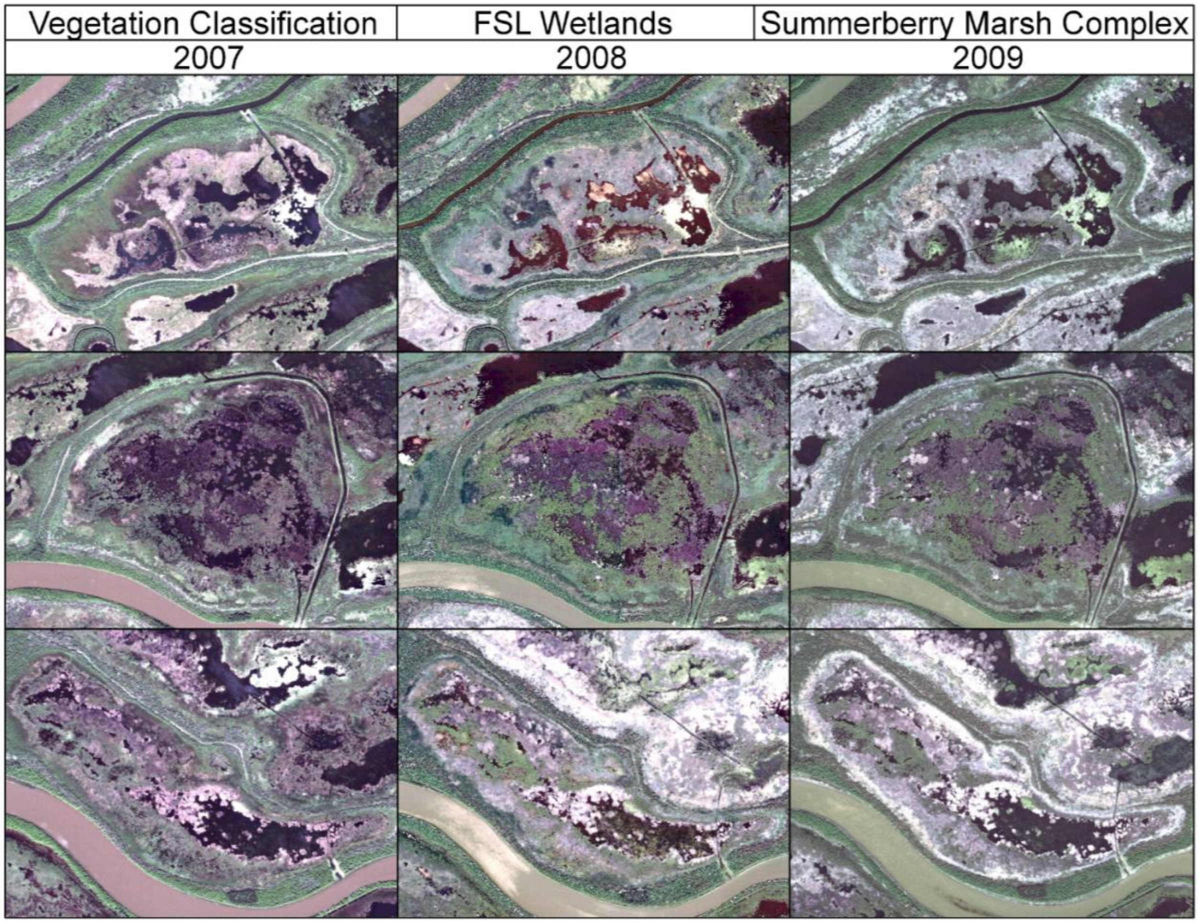

Fig. 7. Quickbird® imagery of full supply level (FSL) wetlands in 2007, 2008, and 2009 at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

The analyses used to select the logistic regression models that classified the segmented polygons produced consistent and accurate results. Backward parameter selection methods produced the most accurate model in nearly all cases (Table 2), although in three of the six groups of models, both stepwise and backwards selection produced the same model. The standard deviation of the NIR band, NDVI, mean NIR, mean green, mean, blue, and depth covariates were always included in the most accurate model (Table 1, Appendix B)

Table 2: Summary statistics of logistic regression models using varying parameter selection methods (no selection, stepwise, forward, and backward) to classify wetland vegetation of full supply level (FSL) and partial drawdown (PD) wetlands at the Summerberry Marsh Complex, The Pas, Manitoba, Canada from 2007-2009.

Year	**Water Level Treatment**	**Parameter Selection Method**	**AIC**	*** Average accuracy (%)**	**Polygons Predicted Correctly (%)**
2007	PD	Stepwise	2082.40	76.79	77.29
	PD	Full	2089.69	76.49	77.02
	PD	Backward	2082.25	76.79	77.29
	PD	Reduced	2528.79	69.74	71.84
	FSL	Stepwise	1941.63	80.51	79.79
	FSL	Backward	1951.67	80.57	80.03
	FSL	Full	1972.64	80.34	79.79
	FSL	Reduced	2412.31	73.69	73.63
2008	PD	Stepwise	1391.41	70.83	85.38
	PD	Backward	1463.39	70.20	84.91
	PD	Full	1588.99	70.50	84.38
	PD	Reduced	1652.77	67.72	82.61
	FSL	Backward	1884.23	82.67	81.29
	FSL	Stepwise	1900.70	82.72	81.29
	FSL	Full	1932.83	82.64	81.16
	FSL	Reduced	2195.71	78.19	76.32
2009	PD	Stepwise	997.06	70.69	91.05
	PD	Backward	997.06	70.69	91.05
	PD	Full	1025.56	72.28	91.36
	PD	Reduced	1234.61	63.57	86.86
	FSL	Full	1614.90	83.36	84.90
	FSL	Backward	1614.90	83.36	84.90
	FSL	Stepwise	1616.62	82.84	84.84
	FSL	Reduced	2036.34	74.67	78.85

Parameter selection methods:
Full - indicates all available parameters were included in the model
Stepwise - indicates forward stepwise parameter selection, SLSTAY p = 0.0001
Backwards - indicates backward stepwise selection, SLENTRY p = 0.0001
Reduced - indicates models built with a subset of parameters

* - Average accuracy calculated by taking the mean (%) accuracy of eight predicted vegetation classes

Overall correct classification was high (Table 2). The senescent vegetation class was consistently predicted with the highest probability, ranging from 0.90-0.99 and averaging 0.966 among PD and FSL wetlands and all years. The *Typha spp.* class was predicted with the lowest probability ranging from 0.52-0.65 and averaging 0.62 among PD and FSL wetlands and all years. Trees, Water, *Scirpus spp.*, *Carex spp.*, *Phragmites spp.*, and *Equisetum spp.* classes were predicted in order from second highest to second lowest prediction accuracy. Prediction probabilities are presented for each wetland and year in Appendix B, Figures 5-10 and Tables 2 and 3.

The resulting classification clearly illustrates the increased amount of senescent vegetation (yellow) in PD wetlands following the partial drawdown in 2007. *Carex* and *Typha*, symbolized as brown and green respectively in Figs. 8-10, were negatively affected by the partial drawdown, and contributed most to the increase in senescent vegetation (Fig. 10). The remaining species classes showed little change in both PD and FSL wetlands, and the proportion of open water did not change in PD or FSL wetlands from 2007-2009

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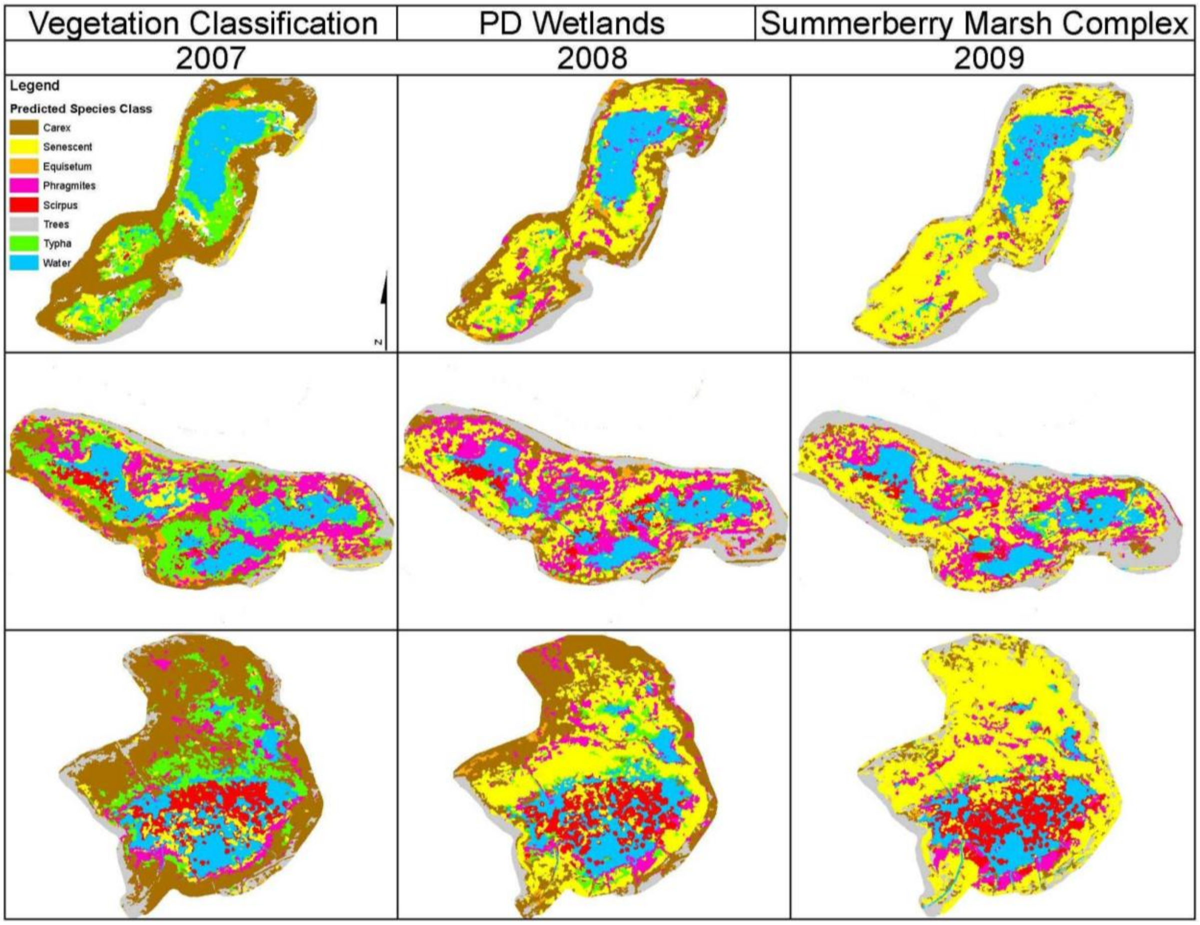

Fig. 8. Classification of wetland vegetation in partial drawdown (PD) wetlands in 2007 (pre-drawdown), and 2008 and 2009 (post-drawdown) at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

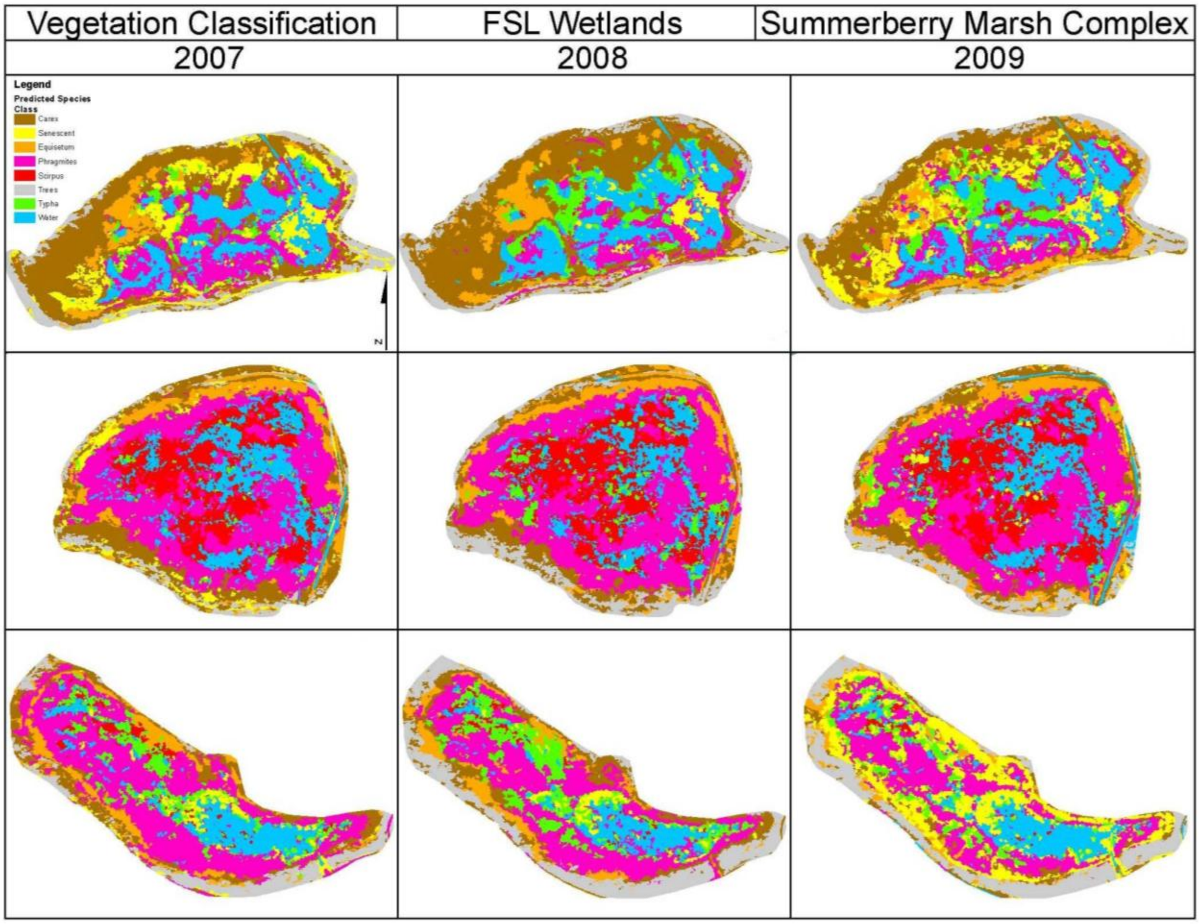

Fig. 9. Classification of wetland vegetation in full supply level (FSL) wetlands in 2007, 2008, and 2009 at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

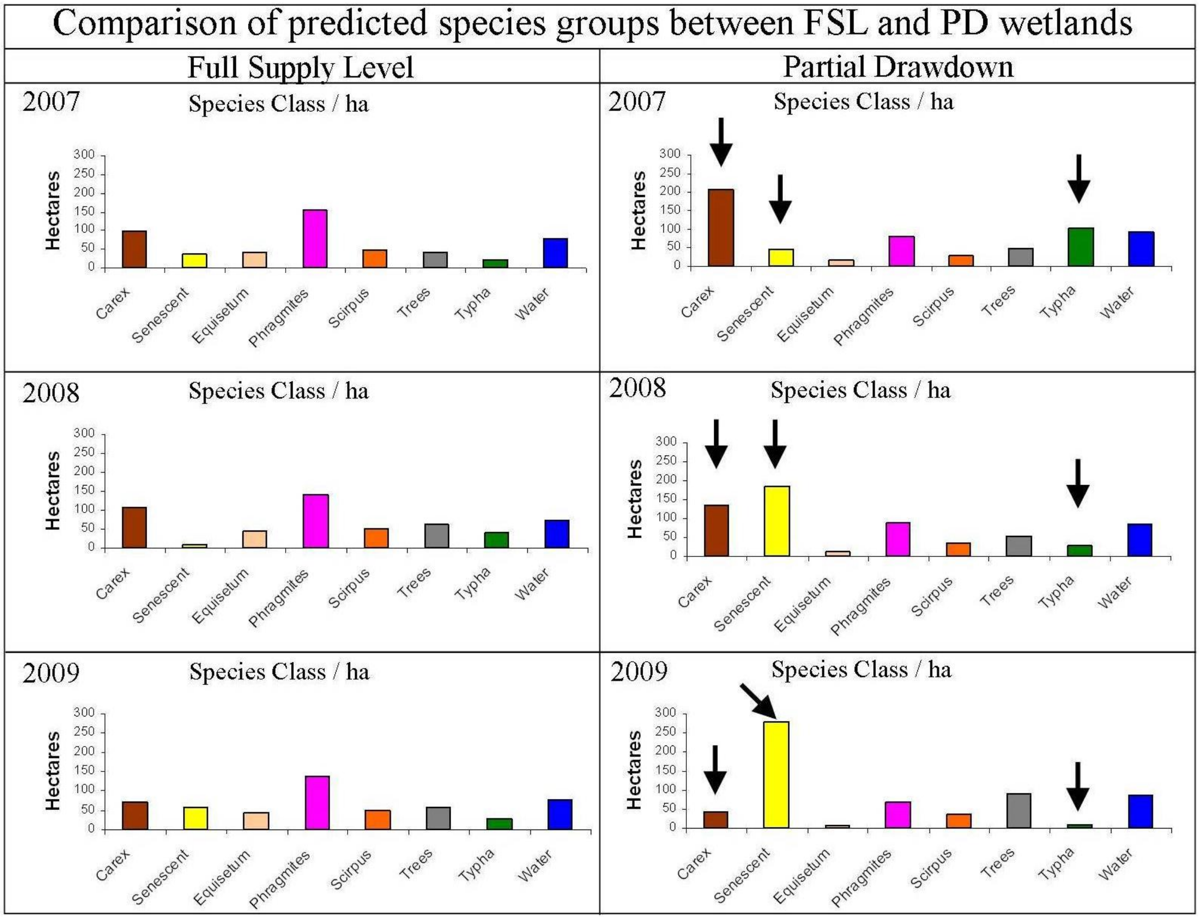

Fig. 10. Changes in ground cover composition full supply level (control) and partial drawdown (treatment) wetlands from 2007-2009 at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

Muskrat House Site Selection - Vegetation Type

Muskrats built active houses in *Equisetum spp.*, *Carex spp.*, and *Phragmites spp.* and *Typha spp.* vegetation types more than they were available, while selecting trees, open water, *Scirpus spp.*, and senescent vegetation less than available (Fig. 11).

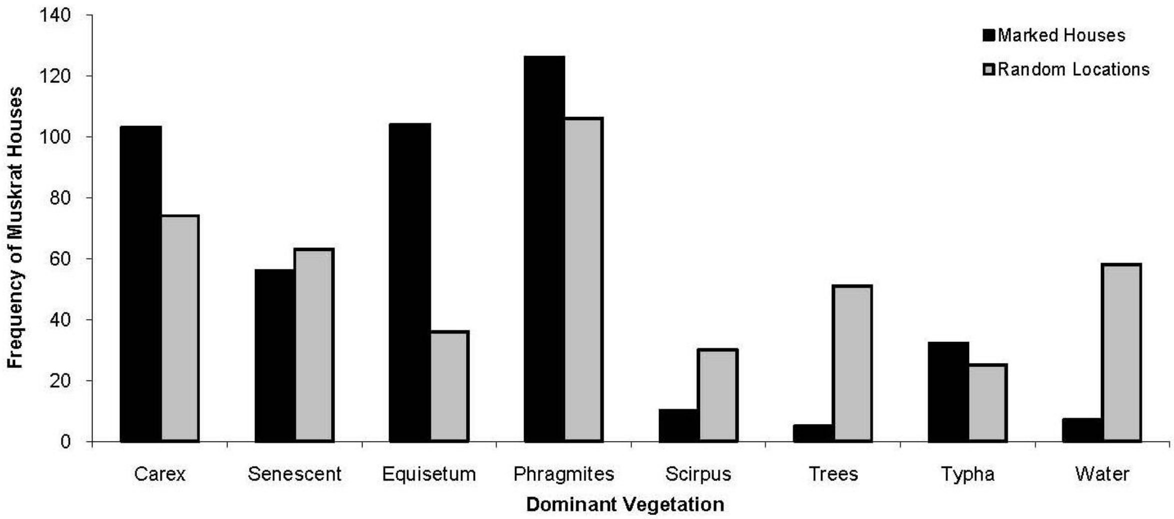

Fig. 11. House site selection by muskrats (*Ondatra zibethicus*) in eight vegetation types at used (marked houses) and available (random locations) sites at the Summerberry Marsh Complex, The Pas, Manitoba, Canada, June 2008-2010.

Habitat Condition and Muskrat House Site Selection

Rooted vegetation was the dominant habitat condition in all wetlands (Fig. 12, Table 3). FSL wetlands had a higher percentage of floating vegetation and lower percentage of rooted vegetation than PD wetlands. The open water habitat condition was essentially the same in both treatment types.

Table 3: Percentage of the landscape covered by different habitat conditions compared across full supply level (FSL) and partial drawdown (PD) wetlands at the Summerberry Marsh Complex, The Pas, Manitoba, Canada in 2009.

Habitat Condition	FSL		PD		Total	
	Hectares	%	Hectares	%	Hectares	%
Water	77.61	14.85	86.34	14.00	163.95	14.39
Rooted Vegetation	358.02	68.50	490.51	79.54	848.53	74.47
Floating Vegetation	87.04	16.65	39.86	6.46	126.90	11.14
Total	522.67		616.71		1139.38	

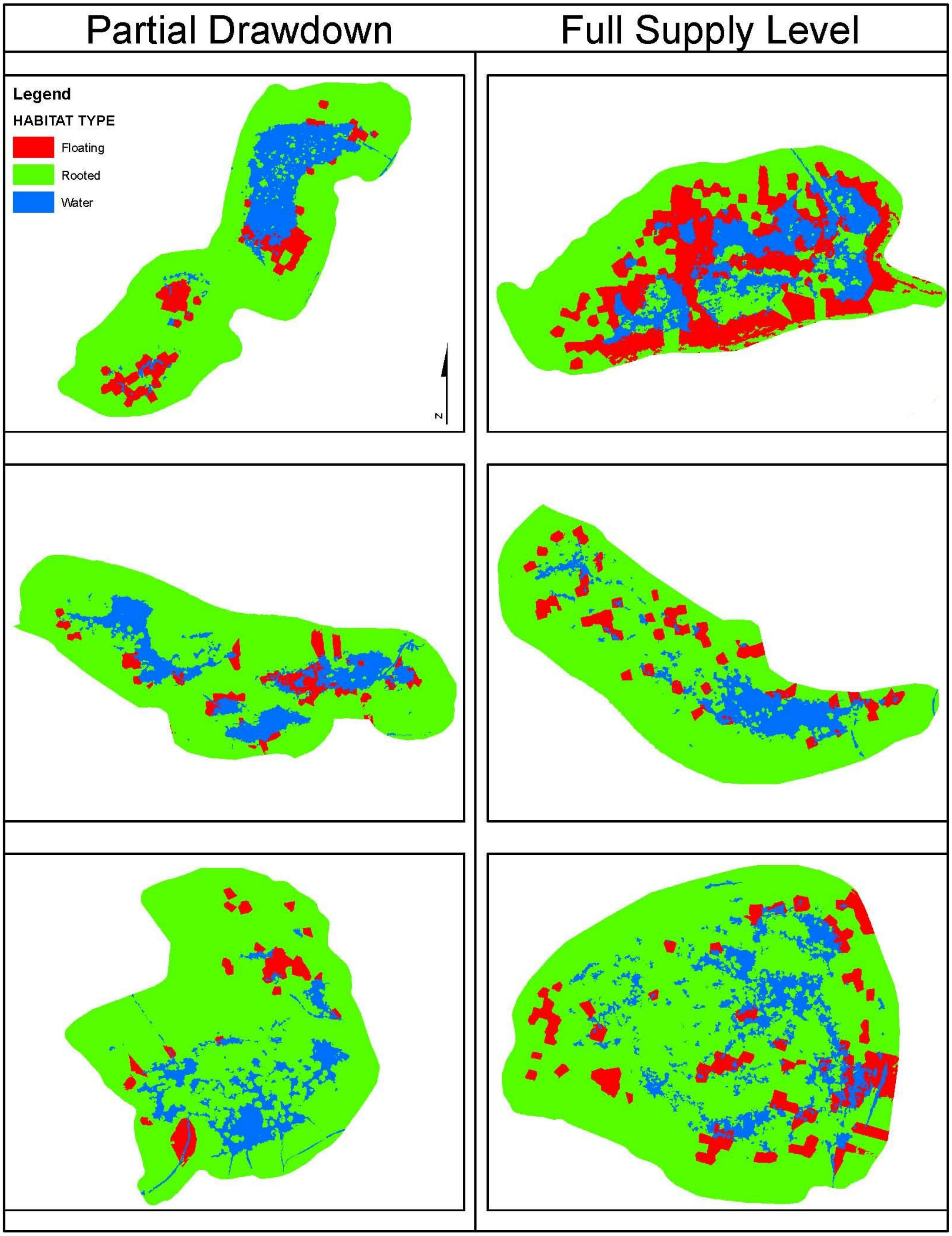

Fig. 12. Delineation of habitat conditions in partial drawdown and full supply level wetlands at the Summerberry Marsh Complex, The Pas, Manitoba, Canada July 2009.

Muskrats built houses in both floating and rooted habitat conditions at a higher proportion than available, and avoided open water conditions (Fig. 13).

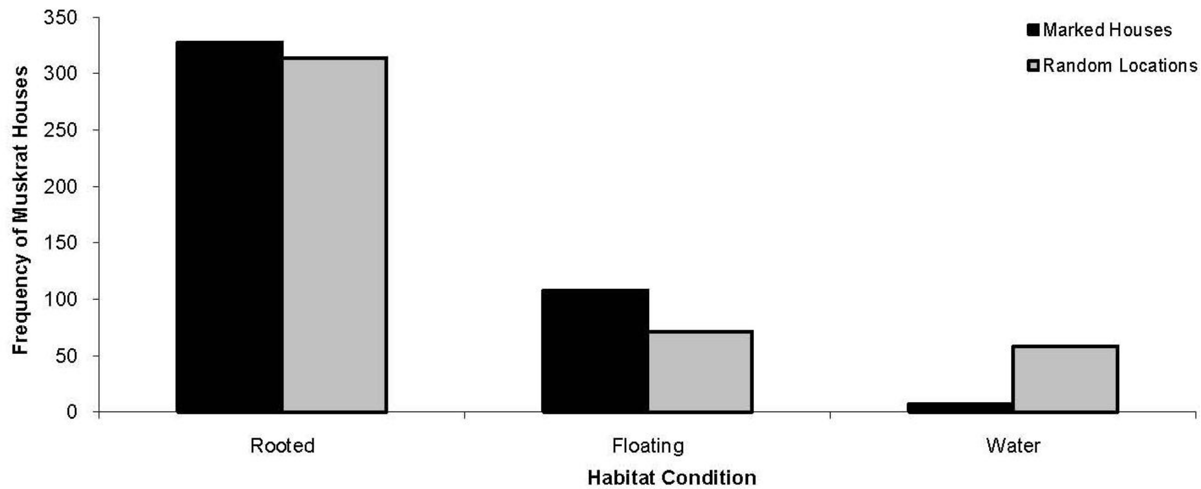

Fig. 13. House site selection by muskrats (*Ondatra zibethicus*) in three habitat conditions at used (marked houses) and available (random locations) sites at the Summerberry Marsh Complex, The Pas, Manitoba, Canada, June 2008-2010.

Univariate tests of covariates

In univariate tests for significance the depth, distance to upland, and distance to trees covariates showed a significant difference between marked houses and random locations, whereas distance to open water was marginally significant, and NDVI and greenness were not significantly different (Table 4). Active houses tended to be in shallower water, closer to upland, closer to open water, and closer to trees than random locations.

Houses in PD wetlands tended to be in shallower water, were closer to upland, closer to open water, further from trees, and had lower NDVI and greenness values than houses in FSL wetlands (Table 5).

Table 4. Means, standard errors (SE), and 95% confidence intervals (LCL and UCL) of continuous habitat variables of random (unused, n = 443) and active (used, n = 443) muskrat (*Ondatra zibethicus*) houses at the Summerberry Marsh Complex, The Pas, MB, Canada 2008-2009.

	House Locations				Random Locations				
Variable	**Mean**	**SE**	**LCL**	**UCL**	**Mean**	**SE**	**LCL**	**UCL**	**Pr (>t)**
Depth (cm)	45.54	1.27	43.04	48.05	49.99	1.27	47.49	52.49	0.01
Distance to Upland (m)	95.59	5.87	84.08	107.10	142.57	5.87	131.06	154.08	<.0001
Distance to Open Water (m)	58.70	3.36	52.11	65.30	67.70	3.36	61.11	74.30	0.06
Distance to Trees (m)	97.26	5.15	87.15	107.37	131.14	5.15	121.03	141.25	<.0001
NDVI	25.17	1.20	22.82	27.52	25.83	1.20	23.48	28.18	0.70
Greenness	0.07	0.01	0.04	0.10	0.07	0.01	0.04	0.10	0.99

Table 5. Means, standard errors (SE), and 95% confidence intervals (LCL and UCL) of continuous habitat variables at active muskrat (*Ondatra zibethicus*) houses in full supply level (FSL) (n = 343) and partial drawdown (PD) (n = 100) wetlands at the Summerberry Marsh Complex, The Pas, MB, Canada 2008-2009.

	FSL Wetlands				PD Wetlands				
Variable	**Mean**	**SE**	**LCL**	**UCL**	**Mean**	**SE**	**LCL**	**UCL**	**Pr (>t)**
Depth (cm)	47.65	0.91	45.85	49.45	38.33	1.69	35.00	41.66	<.0001
Distance to Upland (m)	106.84	4.59	97.82	115.86	57.01	8.50	40.30	73.71	<.0001
Distance to Open Water (m)	67.15	2.49	62.25	72.04	29.75	4.61	20.69	38.81	<.0001
Distance to Trees (m)	91.35	4.21	83.07	99.62	117.56	7.80	102.23	132.89	0.0033
NDVI	27.41	1.34	24.77	30.04	17.50	2.48	12.62	22.38	0.0005
Greenness	0.11	0.01	0.08	0.13	-0.05	0.02	-0.09	0.00	<.0001

Resource Selection Function

Correlation tests between continuous covariates revealed that ‘distance to upland’ and ‘depth’ ($r = 0.74$), and ‘distance to upland’ and ‘distance to trees’ ($r = 0.80$), and ‘depth’ and ‘distance to trees’ ($r = 0.71$) were significantly correlated. Therefore I removed ‘distance to trees’ from consideration in the logistic regression model, however retained ‘depth’ and ‘distance to upland’. I chose to retain the ‘depth’ and ‘distance to upland’ covariates as a model parameters, because both were highly significant in univariate comparisons, the retention of both increases model performance in logistic regression models, and the correlation between the two covariates is below the $r = 0.70$ threshold when considering only PD wetlands.

Preliminary analysis indicated that models with independent vegetation type and habitat condition parameters did not fit the data well. Therefore I merged these variables into one covariate column that collapsed the classes into rooted and floating conditions of *Carex spp.*, *Equisetum spp.,* and *Typha spp.*, etc. along with water. I choose to retain the ‘greenness’ parameter, although it was not significant in univariate tests, because it improved model performance and was always retained in stepwise selection.

The most parsimonious model correctly predicted 84.1% of active muskrat house locations and explained 34% of the variation in the data (Table 6). According to this model active muskrat houses were located most preferentially in rooted *Typha spp.* followed by rooted *Equisetum spp.* (Table 7). Muskrats preferred any vegetation type, whether rooted or floating, over the reference category of open water, but, generally preferred rooted habitat types over floating habitat types. The locations of active muskrat houses were positively correlated with distance to upland and depth, and inversely proportional to distance to open water and greenness. Distance to upland was the most important main effect habitat covariate in predicting the location of active muskrat house locations, followed by the habitat condition and vegetation type covariates.

Table 6: Summary statistics of logistic regression models of muskrat (*Ondatra zibethicus*) house site selection at the Summerberry Marsh Complex, The Pas, MB, Canada 2008 and 2009.

Model Variables	K	Δ AIC	AIC weights	Pseudo R-square	% Concordant
HV, D, DU, DW, G, SP, D*DU, D*DW, D*SP, DU*G	19	0.00	0.56	0.34	84.1
HV, D, DU, DW, SP, D*DU, D*DW, D*SP	18	0.90	0.36	0.34	84.1
HV, D, DU, DW, D*DU, D*DW	14	4.36	0.06	0.33	83.5
HV, D, DU, DW, SP, D*DU, D*DW	16	8.00	0.01	0.33	83.6
Main effects + all interactions of main effects and D	30	11.24	0.00	0.35	84.6
Global - all main effects and all two way interactions	90	52.47	0.00	0.41	87.5
Main effects + all interactions of main effects and HV	70	209.94	0.00	0.26	79.3
* Global - all main effects and two way interactions	18	229.92	0.00	0.15	70.6
All main effects	16	237.19	0.00	0.14	70.8

HV - Habitat and Vegetation; Categorical, 8 classes (i.e. Floating *Carex*, Rooted *Carex*, Water, etc.)
T - Treatment; Categorical, 2 classes (Partial Drawdown and Full Supply Level)
D - Depth (cm)
DU - Distance to Upland (m)
DW- Distance to Open Water Habitat (m)
G - Greenness Index; NDVI reflectance scaled between years where -1 is Water, and 1 is robust vegetation
SP - Sampling Period; Categorical, 3 classes (Spring 2008, Spring 2009, Fall 2009)

* - stepwise selection

Table 7: Estimated coefficients ($\hat{\beta}$), standard errors (SE), and associated probabilities of habitat covariates retained in the most parsimonious model describing the locations of active muskrat (*Ondatra zibethicus*) houses in the Summerberry Marsh Complex, The Pas, Manitoba, Canada 2008-2010.

Habitat Covariates	β Estimate	SE	Odds Ratios	Wald Chi-square	Pr > Chi-square
Floating Carex	1.93	0.60	6.90	10.26	0.0014
Floating Equisetum	2.11	0.64	8.27	10.75	0.001
Floating Other	1.94	0.54	6.94	12.83	0.0003
Floating Typha	1.89	0.66	6.64	8.20	0.0042
Rooted Carex	2.09	0.57	8.09	13.53	0.0002
Rooted Equisetum	2.59	0.58	13.29	19.85	<.0001
Rooted Other	1.78	0.51	5.96	12.19	0.0005
Rooted Typha	2.82	0.68	16.69	16.89	<.0001
Distance to Upland (m)	0.35	0.05	1.42	58.60	<.0001
Distance to Water (m)	-0.20	0.06	0.82	12.76	0.0004
Depth (cm)	0.03	0.01	1.03	4.95	0.0261
Fall 2009	-0.34	0.75	0.71	0.21	0.649
Spring 2009	-1.15	0.43	0.32	7.16	0.0074
Greenness	-1.55	0.71	0.21	4.72	0.0299
Distance to Upland (m)* Depth	-0.01	0.00	0.99	93.02	<.0001
Distance to Water (m)* Depth	0.01	0.00	1.01	16.07	<.0001
Depth*Fall 2009	0.02	0.02	1.02	1.30	0.2549
Depth*Spring 2009	0.03	0.01	1.03	9.79	0.0018
Distance to Upland (m)*Greenness	0.13	0.07	1.14	3.40	0.0651

Nutritional Analysis

Stems had higher acid detergent fiber (ADF) content in all plant types than rhizomes ($F_{[1, 363]}$ = 312.40, P = 0.0001). ADF was significantly reduced by the partial drawdown in *Carex spp.* stems ($F_{[1, 33]}$ = 5.35, P = 0.028) and rhizomes ($F_{[1, 28]}$ = 10.46, P = 0.003), and in rooted *Typha spp.* stems ($F_{[1,43]}$ = 5.62, P = 0.02) (Table 8). No significant difference was detected when all vegetation types were combined for rhizomes ($F_{[1, 187]}$ = 0.71, P = 0.40) or stems ($F_{[1, 172]}$ = 0.28, P = 0.60). Among all plant types, ADF was highest in *Phragmites spp.* rhizomes ($\bar{x}$ = 37.07, $F_{[3, 186]}$ = 158.38, P = 0.0001) and *Phragmites spp.* stems ($\bar{x}$ = 50.16, $F_{[3, 171]}$ = 108.27, P = 0.0001) and lowest in both stems ($\bar{x}$ =37.84) and rhizomes ($\bar{x}$ = 17.63) of floating *Typha spp*. Post hoc Tukey's honestly different test revealed that ADF did not differ between rooted *Typha spp.* floating *Typha spp.* stems (P = 0.99), or rhizomes (P = 0.21).

Table 8: Acid detergent fiber (ADF) content of four plant types consumed by muskrats (*Ondatra zibethicus*) collected from full supply level (FSL) and partial drawdown (PD) wetlands at the Summerberry Marsh Complex, The Pas, Manitoba, Canada September, 2009.

Vegetation Type	Plant Part		FSL			PD		
			n	$\bar{x}$	SE	n	$\bar{x}$	SE
Carex	**Rhizome**	*	11	34.23	1.29	19	29.00	0.98
	Stem	*	16	40.80	0.52	19	39.16	0.48
Phragmites	**Rhizome**		29	38.03	0.97	27	36.04	1.01
	Stem		21	49.79	0.78	27	50.45	0.69
Typha (rooted)	**Rhizome**		22	20.61	1.36	26	18.87	1.25
	Stem	*	20	39.59	0.89	25	36.76	0.79
Typha (floating)	**Rhizome**		31	17.53	0.82	24	17.68	0.93
	Stem		26	38.21	0.95	20	37.31	1.08

***** - means significantly different ($p < .05$) between FSL and PD wetlands

Rhizomes had higher CP content among all plant types than stems ($F_{[1, 454]}$ = 176.28, P = 0.0001). Crude protein (CP) was significantly higher in stems of rooted *Typha spp.* plants in PD wetlands compared FSL wetlands ($F_{[1, 48]}$ = 5.77, P = 0.02) (Table 9). When all vegetation types were combined, no significant difference was detected in CP content of rhizomes between plants in FSL and PD wetlands ($F_{[1, 225]}$ = 0.60, P = 0.44), however stems of plants in PD wetlands had marginally higher CP content than plants in FSL wetlands ($F_{[1, 225]}$ = 3.60, P = 0.059). Floating *Typha spp.* rhizomes in FSL wetlands had the highest CP content among all plant types ($\bar{x}$ = 6.12%), however in post hoc Tukey's honestly different tests did not differ from rooted *Typha spp.* ($\bar{x}$ = 5.98%, P = 0.99), nor *Phragmites spp.* ($\bar{x}$ =

6.00%, $P = 0.99$). Additionally, CP content did not differ between rooted *Typha spp.* and floating *Typha spp.* stems ($P = 0.43$), or rhizomes ($P = 0.99$).

Table 9: Crude protein content of four plant types consumed by muskrats (*Ondatra zibethicus*) collected from full supply level (FSL) and partial drawdown (PD) wetlands at the Summerberry Marsh Complex, The Pas, Manitoba, Canada September, 2009.

Vegetation Type	Plant Part		FSL			PD		
			n	$\bar{x}$	SE	n	$\bar{x}$	SE
Carex	**Rhizome**		30	2.85	0.58	30	3.23	0.58
	Stem		30	1.72	0.27	30	1.47	0.27
Phragmites	**Rhizome**		29	5.90	0.40	30	6.04	0.40
	Stem		29	2.59	0.30	30	3.07	0.30
Typha (rooted)	**Rhizome**		22	6.32	0.50	28	5.71	0.45
	Stem	*	22	2.10	0.33	28	3.14	0.29
Typha (floating)	**Rhizome**		31	6.70	0.44	27	5.52	0.47
	Stem		31	2.02	0.30	27	2.42	0.33

* - means significantly different ($p < .05$) between FSL and PD wetlands

Discussion

Vegetation Mapping

Object based classification proved to be a viable method for classifying emergent vegetation from high resolution satellite imagery. Baschuk (2010) concluded that object based classifications produced higher accuracies than both unsupervised and supervised pixel based classification schemes. Prediction accuracies from models which included a class for senescent vegetation were higher than accuracies produced by Baschuk (2010) which did not include a class for senescent vegetation. I attribute this difference to the vast differences in spectral signatures reflected by senescent vegetation and live vegetation.

Gilmore et al. (2008) used similar methods and produced similar results and prediction accuracies. Similar to Baschuk (2010) and me, they noted that *Typha spp.* was predicted with the lowest accuracies. Interestingly, they included LiDAR© data to distinguish between the canopy heights of the different vegetation classes, which produced high classification rates of *Phragmites*. I presume the intensity of ground truthing needed to produce accurate results could be reduced with the inclusion of additional data sources, such as LiDAR© data. The method could be modified to reduce the amount of effort needed for valid results by relying primarily on remotely sensed data as long as the analyst has knowledge of the area, species can be easily identified from the imagery, and well-designed ground truthing was used to derive prediction probabilities.

Vegetation Changes

Vegetation responses to natural or managed water level changes are well documented in prairie wetlands (van der Valk 2000), however less is known about the dynamics of emergent vegetation in response to water level manipulations in northern deltaic systems. Zonation patterns of emergent macrophytes in the SMC differ from those reported by van der Valk (2000). He lists zonations from furthest up slope (driest) to down slope (wettest)of *Phragmites, Scolochloa, Typha,* and *Scirpus,* where my observation was *Carex, Equisetum,* *Phragmites, Typha,* and *Scirpus.* The most notable difference in zonation is that *Phragmites* appears to grow in deeper habitats, apparently indicating that this species is more flood tolerant in SMC wetlands as compared to the prairie wetlands of Delta Marsh, Manitoba.

In addition to the deeper flood tolerances of *Phragmites,* we did not observe lake stage wetland conditions following the overbank flooding of 2005, and subsequent high water conditions (Figs 1-6, Appendix A). van der Valk (2000) documented the senescence of emergent vegetation which created open lake habitats at Delta Marsh Manitoba following two years of deep (1 m) flooding. Conversely, after two years (2005-2007) of flooding to similar magnitudes in SMC wetlands, open water habitat comprised only 15% of the landscape. Though no baseline data was available from before 2007, subsequent classifications in 2008 and 2009 show no evidence of increased amounts of open water habitat due to deep flooding in FSL wetlands. I estimated that approximately 17% of the landscape in FSL wetlands is comprised of floating mats of vegetation, which may have been caused by the increases in water level following the flood in 2005. Regardless, I estimated that 69% of the landscape in FSL is dominated by rooted emergent vegetation, far more than would be typical in prairie wetlands following two years of deep flooding. These results suggest that the entire vegetative community in the SMC differs in successional patterns in response to water level change, a conclusion that should be of special interest to wetland managers who have previously designed management plans based on the prairie wetland cycle.

Also of significance to vegetation succession in these wetlands is the amount and distribution of senescent vegetation in PD wetlands following the drawdowns. In SMC most of the increase in senescent vegetation was *Carex,* though all species were involved to some degree. It is possible that rhizomes of plants exposed to air during the fall drawdown in 2007 could have freeze dried thus stunting growth or killing the plant entirely.

Compounding those effects, the light brown senescent vegetation likely absorbs less heat than a robustly growing dark green plant or dark open water, further delaying soil temperatures from increasing to temperatures suitable for germination.

Stands of senescent *Typha spp.* in PD wetlands were found in areas where the substrate remained frozen into early August. Additionally, both Carex and *Typha* were the species classes which predominately persisted in floating mats. The effects of insulation and frozen substrate may promote the development of floating mats.

If senescent vegetation is completely dead, it is possible that when the PD wetlands are reflooded the areas of senescent vegetation will revert to open water. Thus PD management will result in a net reduction on aboveground emergent macrophytes and more open water when compared to the pre-drawdown conditions. Alternatively if rhizomes and roots of senescent vegetation survive, the dewatered areas may respond with robust growth in the years following the drawdown. The relationship between water levels and freeze drying of rhizomes, frozen substrates, senescent vegetation, and floating mats is unclear, and could be the focus of future studies of vegetation dynamics in northern deltaic wetlands.

Muskrat House Site Selection - Vegetation Type

In order of magnitude, active muskrat houses were found more frequently than expected in *Equisetum, Typha, Carex,* and *Phragmites,* and less than expected in senescent vegetation, *Scirpus,* and open water habitats. However when controlling for other variables in the RSF, selection was strongest for *Typha* followed by *Equisetum*. The model predicted that active houses are ~17 times more likely to be located in rooted *Typha* habitats than in open water, and ~13 times more likely to be located in rooted *Equisetum* than in open water.

Selection for *Typha* is generally consistent with other studies (Kroll and Meek 1985, Messier et al. 1990, Clark 1994, Clark 2000), however both Messier et al. (1990) and Clark (1994) found muskrats selected for *Scirpus* habitats, whereas I found active houses were found less than expected in *Scirpus* habitats. I attribute this to the differences in vegetation zonation patterns in the SMC wetlands where *Scirpus* was found in relatively deep average water depths of 92 cm in FSL wetlands and 52 cm in PD wetlands, while muskrats selected for depths of 48 cm in FSL wetlands, and 38 cm in PD wetlands.

Finding active houses in *Equisetum* is consistent with studies of other northern climes (Danell 1978, Jelinski 1989). Danell (1978) reported high selection for *Equisetum* was due to seasonally fluctuating water levels in northern Swedish lakes where *Carex spp.* were found upslope and *Scirpus spp.* were found down slope. Jelinski (1989) also found *Equisetum* to be the species most selected for in his study in the Mackenzie River Delta, and credited the high protein values to its selection.

The selection for *Carex* habitats, and the distinct distribution around the wetland in the *Carex* zones of FSL wetlands could be a relic of the over bank flood event in 2005. Muskrats could have shifted activity into this newly flooded *Carex spp.* zone which had the suitable combination of vegetation and water depth. Both Danell (1978) and Jelinski (1989) documented seasonal shifts in the distributions of muskrats to upslope sedge (*Carex*) dominated habitats during the spring months when water levels were high, followed by the down slope migration to deeper *Equisetum* and *Scirpus* habitats. Selection of the *Carex spp.*

zone under these stable water level regimes might be disadvantageous to muskrats because this zone is relatively shallow where winter freeze outs are more likely (Messier et al. 1990, Clark 1994), and it is close to upland where houses are exposed to predation (Clark and Kroeker 1993, Clark 2000).

Muskrat House Site Selection - Habitat Condition

In simple comparisons it appears that muskrats selected for both floating and rooted habitats. However, when other habitat variables were controlled for in the RSF, rooted habitats were selected for with greater frequency than floating habitat types. On average muskrats selected for rooted habitats about 16 times more frequently than open water, while selecting for floating habitats 11 times more frequently than open water. It is reasonable to speculate that floating mats of vegetation offer little stability for the weight of a house and that rhizomes of floating vegetation are more susceptible to freezing in the winter, making them inaccessible as a food resource.

Muskrat House Site Selection – Additional Covariates

In other studies of muskrat habitat use, distance to open water and water depth are often the dominant factors in habitat selection (Clark 2000, Erb and Perry 2003). But in my analyses distance to upland, distance to water, depth, and all interaction terms had marginally small effects on house site selection. Despite small estimates coefficients, the average depth of active housed of 48 cm in FSL wetlands and 38 cm in PD wetlands (overall 45 cm) is only slightly different from the range of 30-40 cm reported in Clark (2000), although slightly greater than those found by Clark (1994) at Delta Marsh, Manitoba. Interestingly, Danell (1978) reported a mean depth of only 20 cm in a northern Swedish lake with similar yearly average temperatures of 0-1° C, comparable to our study site. My observations in the SMC support the importance of water depth in habitat selection by muskrats, but these models accounted for that selection through variables for habitat condition and vegetation type.

Nutritional Analysis

The analysis of nutritional content of plants from the SMC wetlands does not support the idea that muskrats there are nutritionally deprived. The nutritional content was comparable to values reported from South Dakota by Hubbard et al. (1988) and Manitoba by Campbell and MacArthur (1994). Consistently authors document *Typha* as a preferred food resource (Bellrose 1950, Lacki et al. 1990, Clark 2000). Campbell and MacArthur (1994) explain that digestibility and nutrient assimilation by muskrats are highest for *Typha* rhizomes and link its food quality to high rates of habitat selection for *Typha* habitats. This explanation is supported by both the nutrient analyses of SMC plants and the RSF model.

In general we detected no significant differences in ADF and CP between plants in FSL and PD wetlands, indicating the partial drawdown had no overall effect on the nutritional content of plants in each treatment. But when I consider individual species such as *Carex* and *Typha* stems in PD wetlands I found significantly lower ADF content, a fact that would make this plant material more digestible. *Carex* and *Typha* were the species classes which contributed most to the large amounts of senescent vegetation in the study wetlands in early July when the satellite images were taken. The large amount of litter in these areas delayed green up of these species so the plants sampled in PD wetlands in September may have been younger than those sampled in FSL wetlands. This explains the reduced amounts of ADF and greater CP indicating a positive effect on nutritional content as a result of the partial drawdown.

I had suspected there would be a difference in ADF or CP between rooted and floating *Typha,* but did not find it. We observed floating mats of *Typha* which appeared to be stunted in growth, and which senesced sooner in the fall, yet we detected no difference in the nutritional content. Future research should explore how and when the floating habitat condition is formed, and how nutrients are absorbed by *Typha spp.* and other species in the floating and rooted conditions.

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CHAPTER 4: ANALYSIS OF AERIAL MUSKRAT HOUSE SURVEYS AND WETLAND MANAGEMENT IN THE SASKATCHEWAN RIVER DELTA.

A paper submitted to the Canadian Journal of Zoology

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Abstract

Ducks Unlimited Canada (DUC) biologists surveyed muskrat populations via aerial house counts in the Saskatchewan River Delta (SRD) from 1979-1990. I used these data to analyze how muskrat houses densities varied in response to different water level manipulation practices, winter temperature and snow depth, and location within the Saskatchewan River Delta (SRD). The most parsimonious time series mixed effect analysis of variance model quantified muskrat house densities as a function of years after a drawdown and snow depth. Muskrat densities were higher in the second through ninth year after a drawdown compared to the years before a drawdown, and in comparison to wetlands which did not receive a managed water level drawdown . Muskrat house densities were positively correlated ($\beta = 0.0139$, SE 0.005) with increased snow depth. Water level management was an effective wetland management practice to increase muskrat density in the SRD.

Introduction

Before hydroelectric development (pre-1960's), the Saskatchewan River flooded at The Pas, Manitoba bi-annually (Fig. 1), once following local ice melt in early spring, and again in July when water from the Rocky Mountain snow melt arrived. These flood waters periodically inundated the surrounding deltaic wetlands and such rapid fluctuations in water levels made habitat conditions variable for muskrats (*Ondatra zibethicus*) and other wildlife. Rapid rises in wetlands inhabited by muskrats can flood houses and displace muskrats, and, conversely, rapid reductions in water levels, or droughts, can also make habitat unsuitable during a drought. Deltaic wetlands are inherently dynamic systems, which makes it difficult to manage fur harvests, especially to keep yearly fur yields sustainably high. But, in the 1930's, economic stress and the relatively high value of muskrat fur, and low water levels, prompted interest in habitat manipulation designed to promote muskrat production in the Saskatchewan River Delta (SRD) (Smith and Jones 1981).

Water control structures were built throughout the SRD during the 1940's to stabilize then unregulated water levels of the Saskatchewan River in SRD wetlands for muskrat production. Following the drought of the late 1930's (Fig. 1a), these water control structures impounded and stabilized water on newly regenerated wetland habitats, and muskrat populations boomed (Fig. 2). McLeod (1950) documented an increase in muskrat house counts in the southeastern portion of the SRD at the Summerberry Marsh Complex (SMC) following the construction of water control structures, and a subsequent decline in populations through the 1950's. Recent data from aerial house counts conducted in winter 2009 suggests muskrat densities in the SRD to be <1/ha (Figs. 3 and 4). Although house counts do not perfectly reflect population levels (Clark 2000) recent house counts generally suggest lower population levels than McLeod (1950) and densities reported in prairie ecosystems (Errington 1963, Proulx and Gilbert 1983, Clay and Clark 1985, Erb and Perry 2003).

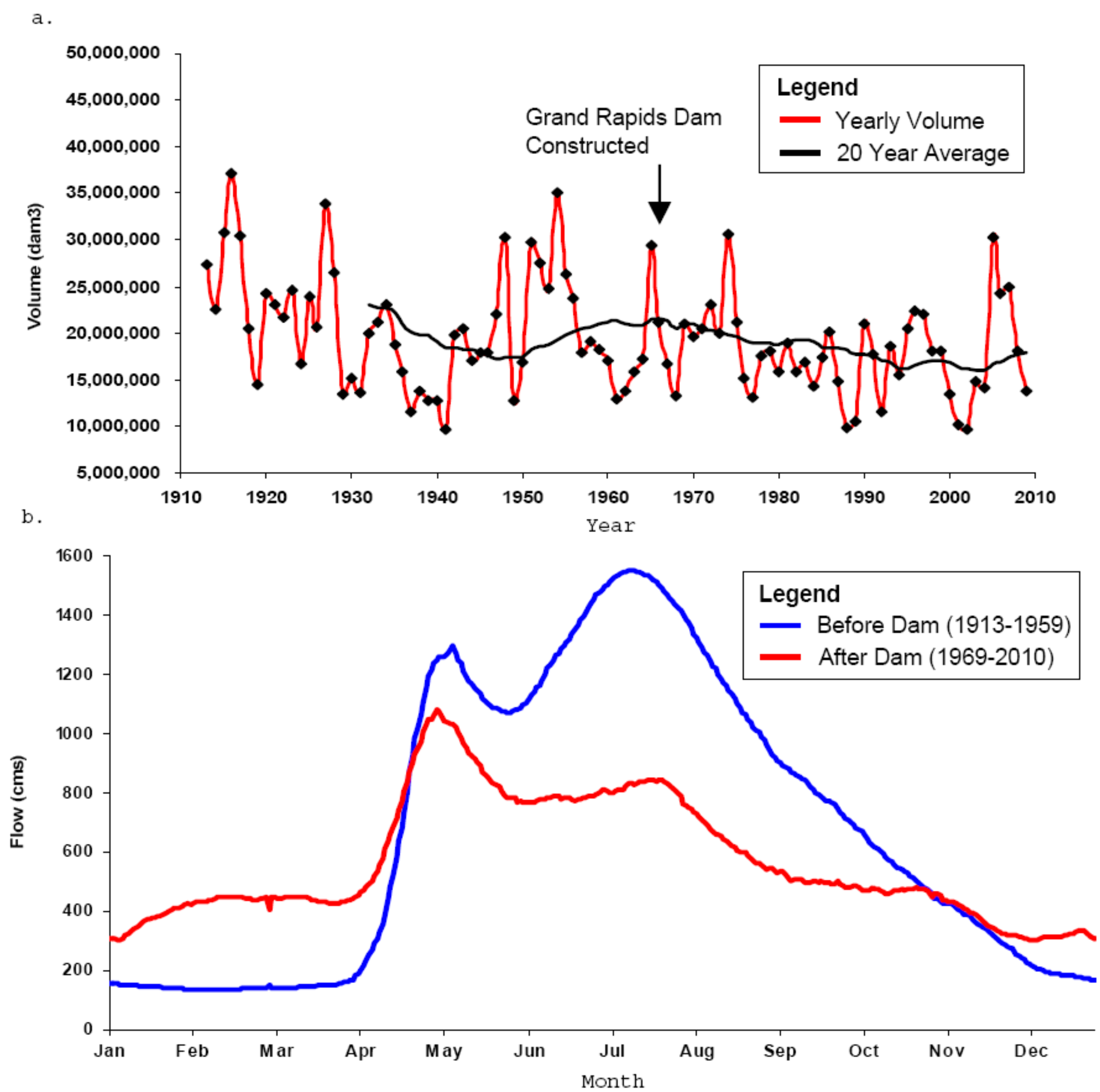

Fig. 1. (a) Total yearly flow of the Saskatchewan River at The Pas, Manitoba, Canada for the past 100 years. (b) Mean weekly flow of the Saskatchewan River at The Pas, Manitoba, Canada before and after the construction of the Grand Rapids Dam in 1968.

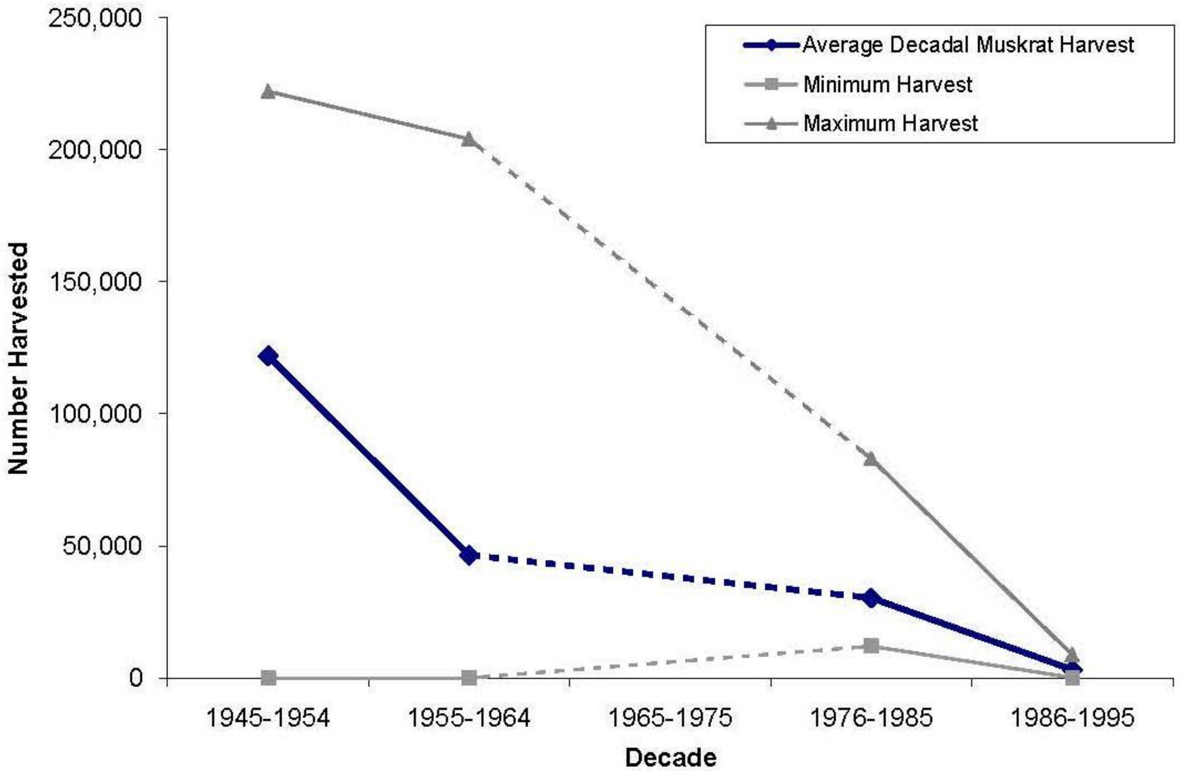

Fig. 2. Muskrat (*Ondatra zibethicus*) harvests by decade in the Saskatchewan River Delta, no point estimates are available for 1965-1975 due habitat changes caused by the closing of the Grand Rapids Hydroelectric Dam and sparse data for that period.

Since the 1960's, hydroelectric developments on the Saskatchewan River have reduced the frequency and magnitude of flood events at The Pas, Manitoba (Fig. 1), and also affected flows both upstream and downstream of the SRD. Reductions in the magnitude of flooding have reduced the frequency of overbank flood events, which historically inundated wetlands with river flood water. This fact, in combination with increased cost and strict regulations on pumping, have made managers reluctant to draw down wetlands, in fear of not having enough water supply or money to reflood. Therefore, the water control structures designed for draw downs to regenerate wetland habitats now impound water thus promoting degenerating wetland conditions throughout the SRD. Long term water level stabilization, as apparent in the SRD, reduces wetland productivity and muskrat abundance (McLeod 1950, van der Valk and Davis 1978, Erb and Perry 2003, Toner et al. 2010).

Documenting population changes is essential to managing muskrat populations (Perry 1982). Aerial house counts are commonly and efficiently used to assess trends in muskrat populations over large areas and many years (Dozier 1948, Mcleod 1948, Proulx and Gilbert 1983). However, because conversion of house counts to population estimates is difficult (Proulx 1984, Clark 2000, Erb and Perry 2003), care in interpretation of the results is necessary. For example, distinguishing active and inactive houses during aerial house counts is subjective but may directly bias population estimates (Proulx and Gilbert 1983, Proulx 1984). In this analysis I do not attempt to estimate absolute muskrat population densities, but only compare trends in muskrat house density over time with regard to wetland management practices, weather conditions, and location in the SRD.

Water level manipulation is the primary muskrat management technique (Erb and Perry 2003). Muskrat populations respond to natural fluctuations in water level (Errington 1963, Clay and Clark 1985, Erb and Perry 2003) and water level manipulations imposed by managers (Kroll and Meeks 1985, Clark 2000, Erb and Perry 2003, Toner et al. 2010). This is primarily because periodic droughts, or managed drawdowns, can re-establish emergent vegetation used by muskrats as food or to build houses (Weller and Frederickson 1973), and increase the reproductive rates of muskrats (Kroll and Meeks 1985). Although beneficial in the long term, drawdowns can result in complete elimination or partial reduction in muskrat populations during the drawdown (Errington 1961, Clark 2000). Upon reflooding rapid invasion of new habitat is typical, and muskrat populations appear to reach peak population levels 3-5 years following reflooding (Kroll and Meeks 1985, Clark and Kroeker 1993, Clark 2000).

Ninety nine water control structures are present in the SRD, which provide varying degrees of water level manipulation capability, from complete drawdown in some, to partial drawdown in others. DUC implemented 15 wetland drawdowns in the SRD from 1979-1990 to attempt to regenerate wetland habitat for waterfowl and muskrat production. During this 12 year time span they conducted aerial house count surveys in 33 wetlands, including wetlands where water level was managed, and also wetlands where water level was not managed. These house count data were summarized in a series of DUC yearly reports which contain house counts, water levels, and management practices (Smith 1981-1982, Smith 1983-1986, Pillipow 1987-1990). House counts were not conducted from 1990-2005, but were reinitiated in 2006 and have been carried out yearly since. I test two hypotheses about how muskrat populations in the SRD responded to water level manipulation.

The SRD is split into two sections by a moraine which runs north and south, where the town of The Pas is located (Fig. 3). Before the construction of the Grand Rapids Hydroelectric dam the lower 1/3 of the delta was presumed to be the most biologically productive area in the delta (Harper 1975). With the closing of the Grand Rapids dam in 1968 this area was inundated by what is now Cedar Lake, and many deltaic wetlands were converted to a permanently flooded lake ecosystem. Today the perception of local resource users is that the upper portion of the delta (CRT and RR complexes), especially Lake 6 and Saskeram areas, are the most productive basins for muskrats.

Winter weather conditions are presumed to affect overwinter survival. Cold winter temperatures, as apparent in the SRD (average mean temperature Oct-April at The Pas, MB from 1971-2000 was -9.53°C (Environment Canada 2010)), can reduce overwinter survival. Winter 'freeze-outs' can occur in northern climates when temperatures are cold enough to permit freezing to the substrate, which prohibits muskrats from accessing rhizomes of emergent vegetation (Clark and Kroeker 1993). Snow depth is assumed to effect survival because snow trapped in vegetation can act as an insulator reducing ice thickness and preventing freezing of the substrate (Messier et al. 1990, Clark 1994).

Muskrats play an important role in wetland ecosystems, therefore an understanding of how muskrat populations respond to water level manipulation is essential in understanding the ecology and management of any wetland ecosystem in which they are present or desired. Local interest in muskrats as a food, fur, and recreational resource have prompted interest in understanding how muskrat populations respond to water level management in the SRD.

This study focuses on testing four primary hypotheses. (1) Drawdown type (complete, partial, or no drawdown) affected muskrat density so that wetlands which received complete drawdowns saw the highest average muskrat house densities, wetlands that received partial drawdowns had lower average house densities, and wetland with no drawdown had the lowest average densities. (2) Drawdowns affected muskrat house density so that the years after a drawdown had higher densities than the years before a drawdown. (3) Wetlands upstream of The Pas (CRT and RR complexes) had higher muskrat densities from 1979-1990 than wetlands downstream of The Pas (SMC). (4) Overwinter conditions (Oct-Apr) of the previous year affected the muskrat house density of the next year's survey so that winters with colder temperatures and smaller snow depth negatively affected muskrat house density.

Study Area

The Saskatchewan River Delta (SRD) is the largest inland delta in North America, spanning eastern Saskatchewan and western Manitoba covering approximately 9950 km^2 near The Pas, Manitoba, Canada. Annual daily mean temperature at The Pas, Manitoba from 1971-2000 was 0.1°C, and 162 days per year had a snow depth of at least 1cm. From 1979-1990 the mean temperature from October through April was -9.4°C and the mean monthly snow depth from Oct-April was16.21cm (Environment Canada, 2010). Aerial house counts were conducted on 33 wetlands basins in the SRD including the Carrot River Triangle (CRT), the Reader-Root Complex, and the SMC (Fig. 3). The flooded area of the wetland basins varied both physically and temporally. Temporal variation in flooded area was dependent on the managed water levels, and ranged from 0 ha, during complete drawdowns, to 7838 ha when the largest basin in physical size was refilled to full supply level (FSL).

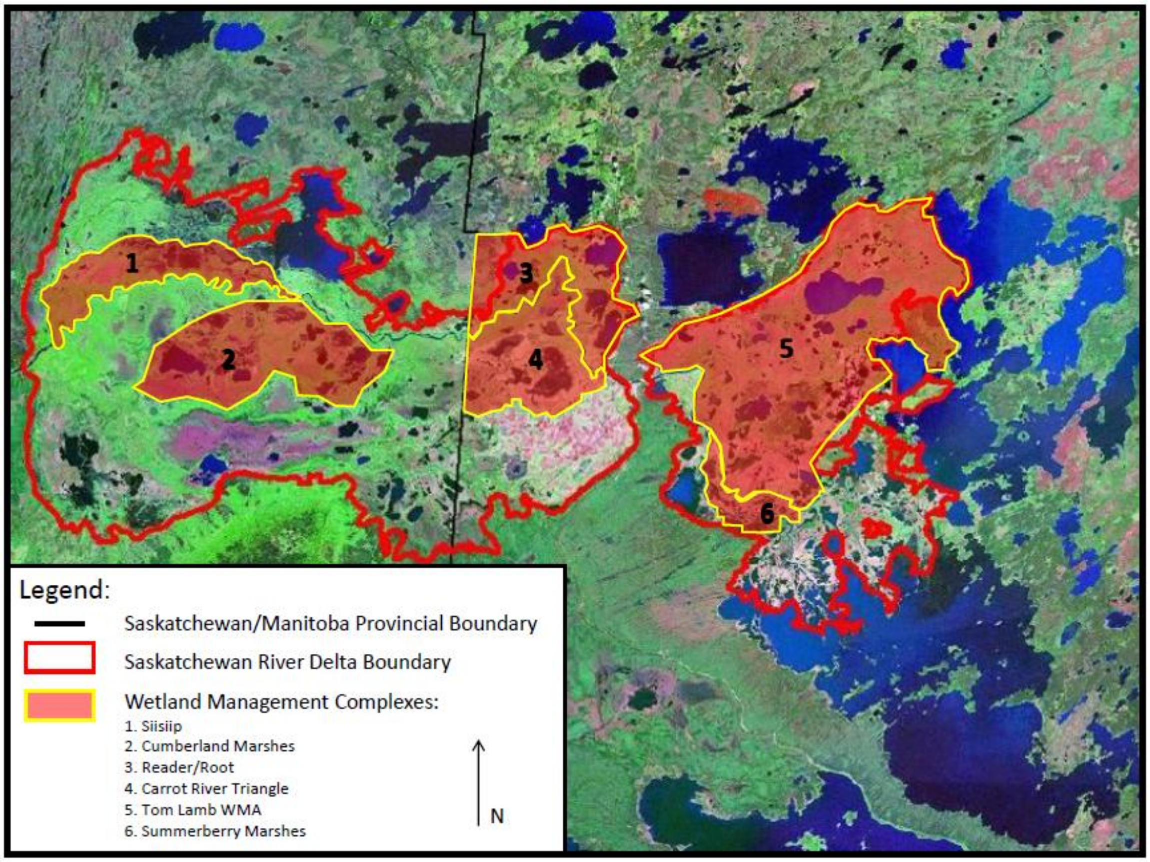

Fig. 3. Map of the Saskatchewan River Delta showing six wetland complexes where water level management and annual muskrat house counts occurred. I report data from wetland complexes (3) Reader Root, (4) Carrot River Triangle, and (6) Summerberry Marshes from 1979-1990.

Methods

Aerial House Counts

Each wetland basin was surveyed once per year from 1979-1990. Although methods varied somewhat from years to year, surveys were ideally conducted on days with clear skies, and after wetland freeze-up with approximately 10-15 cm of snow covering the ice. Each wetland basin was surveyed from a fixed wing aircraft with one or two observers. Two observers were used to count larger basins, or basins with high muskrat house densities. Each observer counted houses independently from the same side of the aircraft using a hand counter, with the sun at the observers back. In cases where two observers were used the highest number recorded by either observer was reported. Basins were counted while flying 50-100 m above the ground at speeds of 80-100 km/h. On large basins requiring multiple passes transects were defined to count the central portions of such basins. Transects through the central portions of large basins were flown at altitudes 450-600m above the ground to allow observers to count larger areas.

I converted house counts from each basin to house density per hectare by comparing water level readings taken at the time of each survey to the ground surface contours provided by DUC's engineering staff. The area used to calculate density represents the flooded area of each basin at the time of survey, and therefore differs from year to year, among and within basins, depending on physical size and water levels. Wetland basins were counted during the years of a drawdown and the data from these instances represents the density of houses at the time of survey, given the reduced water levels and flooded area.

The primary difficulty of monitoring muskrat populations via aerial house counts is accurately identifying houses, or dwelling structures, from feeding platforms or 'push ups' (Erb and Perry 2003). Muskrats build feeding platforms and 'push-ups' of similar vegetation used in houses, however, these structures are not dwellings. Feeding platforms and push-ups are much smaller than houses and are identifiable from the air and are not included in this analysis. Further complication and inaccuracy exists in determining whether houses are 'dead' (i.e. not currently occupied by muskrats) or 'live' (i.e. currently inhabited), which is not identifiable from the air, and is in no way corrected for in this analysis. For this analysis I assume all the houses which were counted to be occupied at the time of survey, and that changes in house densities from year to year represent changes in muskrat populations.

Statistical Analysis

I modeled the time series of muskrat house counts as a multivariate response of management practices and important environmental variables (Fig. 4). Each individual basin is identified by a 'basin' covariate containing the basin name.

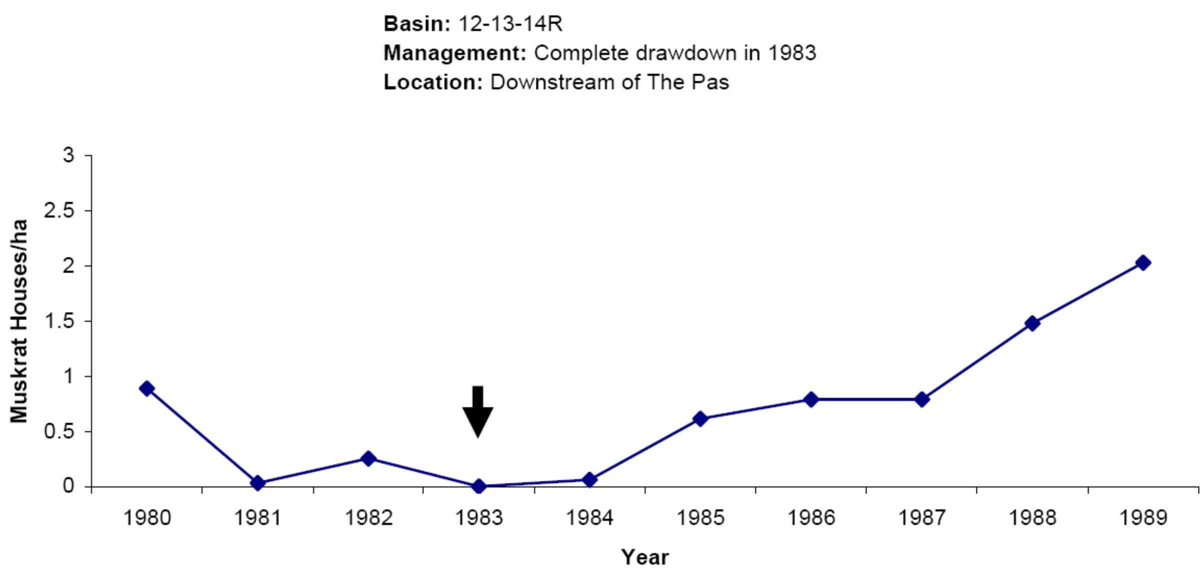

Fig. 4. Muskrat (*Ondatra zibethicus*) house counts of wetlands 12-13-14R from 1980-1989 in the Saskatchewan River Delta.

I analyzed how various water level management techniques effected muskrat house densities using several variables. I analyzed how muskrat house densities vary in response to the type of water level management by including a categorical variable for 'management type'. This covariate was coded as 'no drawdown' for wetlands that did not receive any water level management, 'partial drawdown' for wetlands that were drawndown to levels where >25% of the basin remained flooded , or 'complete drawdown' where water levels were drawndown so that <25% of the basin remained flooded. This 'drawdown type' parameter compares how different management practices affect muskrat house densities, however, does not account for the temporal effects of a drawdown.

To account for temporal effects on how the years after a drawdown might affect muskrat house densities I added a 'years since drawdown' parameter. The values for this covariate are coded such that the years before a drawdown and the year or years of a drawdown are zero values, and the years after a drawdown have positive integer values which progressively increase by one for each year after a drawdown. Wetlands which received no drawdown were coded as zero for all years. I tested for linear effects of the 'years since drawdown' parameter, which assumes a constant linear trend in muskrat house density following a drawdown (Fig. 4). I also tested for separate effects of each year after a drawdown, which allows the magnitude of the effects of the drawdown to vary from year to year after a drawdown (Fig. 5). Once I determined if linear or separate 'years since drawdown' effects fit the data better, I included an interaction term for 'type of management*years since drawdown' to determine if the type of management affected the temporal effects of management.

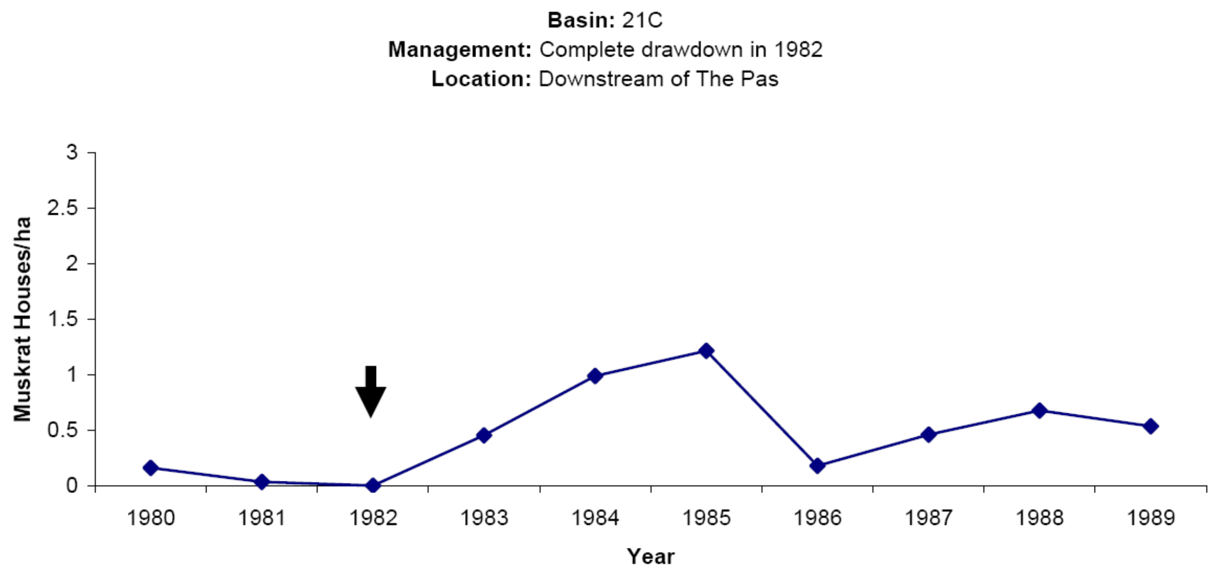

Fig. 5. Muskrat *Ondatra zibethicus*) house counts of wetlands 21C from 1980-1989 in the Saskatchewan River Delta.

Wetland basins upstream of The Pas are currently reported to be more productive in terms of muskrat production by local resource users. I tested this hypothesis by adding a parameter, ‘location’, to my model. Each wetland basin has a categorical attribute for the location parameter, either ‘upstream’ of the town of The Pas for the CRT and RR complexes, or ‘downstream’ for all SMC wetlands. This parameter tested whether or not basins upstream of The Pas, had higher muskrat houses densities from 1979-1990.

Overwinter weather conditions can affect muskrat survival (Messier et al. 1990, Clark and Kroeker 1993, Clark 1994, Clark 2000). I tested the hypothesis that overwinter conditions (Oct-Apr) of the previous year affected the muskrat house density. I expected that winters with colder temperatures and less snow depth negatively affected muskrat house density in the subsequent fall. I used measurements from the previous winter because if overwinter conditions reduced survival, fewer muskrats would be available to build houses the next fall. I added three variables with continuous values to my model, all of which use measurements taken at The Pas, Manitoba by Environment Canada (Environment Canada 2010). The first variable was 'last year's mean overwinter temperature'. I calculated the values for this variable by taking the average of the mean monthly temperatures (°C) from October through April for each year. The second variable was 'last year's mean snow depth'. I calculated the values for this variable by taking the average of the mean monthly snow depth from October through April for each year. The third variable is the interaction of 'last year's mean overwinter temperature' and 'last year's mean snow depth'.

Additionally, since wetlands upstream of The Pas are generally deeper than those downstream of The Pas, I tested the interaction between 'location' and 'last years mean overwinter temperature', and the interaction of 'location' and 'last year's mean snow depth'. Since the upstream basins are generally deeper, overwinter conditions should have less of an impact on muskrat populations when compared to basins downstream of The Pas. These variables tested if harsh overwinter conditions (i.e. low temperatures and low snow depth) impacted muskrat density in the SRD from 1979-1990, and if the affects of overwinter conditions differ by location.

I built linear models using Proc Mixed in SAS 9.2 (SAS Institute Inc. Cary, NC, USA). Individual basins were modeled as random effects, with the location and management effects nested within each basin. Overwinter effects were treated as fixed effects. I compared models using Akaike's Information Criterion, corrected for small sample size (AIC_c; Burnham and Anderson 2002). I examined a studentized residual plot of the best model to look for (1) patterns not explained by the model parameters, and (2) increased variability.

Results

Not all basins were surveyed consistently so I removed years 1979 and 1990, and the basins Root Lake, Rocky Creek, Nestle, Watseskwatapi, Barrier Lake, Wing Lake, and Rae Lake due to missing observations. The remaining reduced data set contained 251 observations from 26 wetland basins surveyed yearly from 1980-1989. Of the 26 basins surveyed, five underwent complete drawdowns, nine underwent partial drawdowns, and eleven basins had no management drawdown during the study period. The flooded surface area used to calculate house density ranged from 0 ha in wetland basins in complete drawdown at the time of survey to 7838 ha (Appendix C, Table 1).

The model which contained parameters for years since drawdown, with year effects modeled separately, and average snow depth was the most parsimonious model of my candidate models (Table 1). Model weight was 99% indicating strong support for this model from among my candidate models. Models with 'years since drawdown' modeled separately for each year always had lower AIC_c compared to models which assumed a linear trend in muskrat house density following a drawdown.

The model which considered the interaction between years since drawdown and the type of drawdown failed to converge in the reduced data set, however the same model did converge when applied to the full data set (i.e. all 33 basins surveyed from 1979-1990) and ranked seventh in AIC_c. In that model, 'years since drawdown' effects did not differ between partial and complete drawdown management practices.

The 'type of management' parameter, which tested for differences in muskrat house density between wetlands with no drawdown, a partial drawdown, or a complete drawdown, was not retained in the best model (Table 1). Muskrat densities in basins which received management (either partial or complete drawdown) ($\bar{x}$ = 0.38, SE = 0.07) did not differ from basins which received no management ($\bar{x}$ = 0.50, SE = 0.07) ($t_{[23]}$ = -1.31, P = 0.202). Muskrat densities in basins which underwent complete drawdowns ($\bar{x}$ = 0.37, SE = 0.07), did not differ from basins which underwent partial drawdowns ($\bar{x}$ = 0.39, SE = 0.09), (t = -0.19, P = 0.852). Muskrat house densities were reduced during the years of a drawdown in all basins which received management. House density was reduced to zero during the years of a drawdown in 10 of the 15 basins, representing 9% of the observations in managed basins (Fig. 5). The observations made during any drawdown represent 13% of the total number of observations in managed basins, and for each basin represents 10-20% of the observations made for a particular basin.

The parameter for 'last year's mean overwinter temperature' was not retained in any model, nor was location. Muskrat densities in basins upstream of The Pas (i.e. RR and CRT complexes) were not higher ($\bar{x}$ = 0.37, SE = 0.09), than in basins downstream (i.e. SMC wetlands) ($\bar{x}$ = 0.45, SE = 0.05), from 1980-1989 ($F_{[1, 24]}$ = 0.85, P = 0.367).

Table 1: Summary statistics of candidate regression models used to explain how wetland management practices, wetland location, and weather covariates affected muskrat (*Ondatra zibethicus*) house density in the Saskatchewan River Delta from 1980-1989.

Model Variables	**K**	**AICc**	**Δ AICc**
YSD1, S	10	259.6	0
YSD1, T, S, T*S	12	271.1	11.5
L, YSD1, T, S, L*T, L*S	17	272.5	12.9
L, YSD1, T, S, T*S	13	273.1	13.5
TM, YSD1, T, S, T*S	13	274.8	15.2
L, TM, YSD1, T, S, T*S	14	276.2	16.6
L, TM, YSD1, YSD1*TM, T, S, T*S	21	*n/a	n/a
L, TM, YSD2, YSD2*TM, T, S, T*S	7	320	60.4
L, TM, YSD2, T, S	5	449.4	189.8
L, TM, T, S	4	491.3	231.7

L - location (upstream or downstream of The Pas
YSD1 - years since drawdown, year effects modeled separately
YSD2 - years since drawdown, year effects modeled as linear effects
TM - type of management (no drawdown, partial drawdown, complete drawdown
S - mean overwinter snow depth
T - mean overwinter temperature
T*S - interaction term of temperature and snow pack

* - model did not converge

According to the most parsimonious model muskrat house densities respond positively in the years after a drawdown and to increased amounts of snow (Table 2). In a given basin, in the first year after a drawdown, muskrat house densities were not different from the years before a drawdown, or from wetland basins that received no management. Years two through seven after a drawdown showed positive effects of drawdowns, when compared to the years before a drawdown, or basins that received no drawdown. The largest effect occurred three years after a drawdown ($\hat{\beta}$ = 1.05) (Table 2). Only two observations were available for eight years after a drawdown and only one observation for nine years after a drawdown, so, although these estimates are highly positive, they should be interpreted with caution. Increasing snow depth positively affected muskrat house density ($\hat{\beta}$ = 0.014) so that for every 10 cm increase in snow, muskrat house densities increased by 14%.

Table 2: Estimated coefficients ($\hat{\beta}$), standard errors (SE), and associated probabilities of explanatory covariates retained in the most parsimonious model describing muskrat (*Ondatra zibethicus*) house densities in the Saskatchewan River Delta from 1980-1989.

Effect	β Estimate	SE	DF	t	Pr > |t|
1 year since drawdown	0.029	0.083	14	0.35	0.734
2 years since drawdown	0.383	0.125	13	3.07	0.009
3 years since drawdown	1.050	0.501	12	2.09	0.058
4 years since drawdown	0.535	0.227	11	2.36	0.038
5 years since drawdown	0.378	0.133	9	2.84	0.019
6 years since drawdown	0.797	0.209	6	3.81	0.009
7 years since drawdown	0.458	0.132	5	3.47	0.018
* 8 years since drawdown	1.079	0.225	1	4.80	0.131
* 9 years since drawdown	1.431	0.225	144	6.35	<.0001
Snow Depth	0.014	0.005	144	2.73	0.007

* - years 8 and 9 since drawdown should be interpreted with caution due to small sample sizes

Discussion

Water level drawdowns were successful at increasing muskrat house densities in the years after a drawdown, however the ten year densities were unaffected. I found no difference in the effects between partial and complete drawdowns on muskrat densities, and the responses to management were variable between wetlands. Regardless of type of drawdown, muskrat houses densities always increased and peaked three years after a drawdown. Snow depth and muskrat house densities are positively correlated, however temperature and location had no effect on muskrat house densities. Water depth and vegetation covariates were not considered, but are important to muskrats and should be considered in future analyses.

The average density of muskrat houses did not increase in basins which received management because, during the years of a drawdown, the densities were reduced enough to offset the increase in densities which occurred after drawdowns. The partial reduction or complete elimination of muskrats during drawdown, or natural drought, is typical (Errington 1961, Clark 2000, Kroll and Meeks 1985). Conversely, in basins which received no management, house densities remained stable, though low, throughout the study period (Appendix C, Fig.3). As a result the mean house density over the study period did not differ between basins which received a management drawdown and those which did not.

I hypothesized that complete drawdowns would confer a greater benefit to muskrats than partial drawdowns, though I found no difference. Nutrient cycling (Murkin et al. 2000b) and vegetative response (van der Valk 2000) should have been greater in wetlands which received complete drawdowns since more substrate was exposed to facilitate decomposition and seed germination. No data exist on nutrient cycling in response to drawdowns in the SRD, however Smith and Jones (1981) detailed the vegetative response of these drawdowns. They noted a large response of *Carex spp.*, *Phragmites spp.*, and *Scirpus spp.*, but only minimal response of *Typha spp.* in basins which underwent complete drawdowns. Partial drawdowns were implemented thereafter in basins where the goal of management was not to increase the amount of emergent vegetation.

Kroll and Meeks (1985) attribute variability in the magnitude of response of muskrat populations to drawdown management to the type of vegetation stimulated by the drawdown. They noted the largest increases in muskrat populations in basins dominated by *Typha spp.*, a preferred food by muskrats, and also noted emigration of muskrats from basins with less desirable food to basins dominated by *Typha spp.* Therefore, since complete drawdowns appear to have stimulated the growth of less desirable vegetation, and partial drawdowns stimulated little vegetative response at all, muskrats responded similarly to both management practices.

The temporal effects of water level management on muskrat populations in the SRD are similar to other areas. Muskrat densities appear to have peaked three years following a drawdown. Clark and Kroeker (1993) reported peak muskrat responses 3-5 years following managed drawdown at Delta Marsh, Manitoba, and Kroll and Meeks (1985) reported peak muskrat responses three years following managed drawdowns in Lake Erie coastal marshes in Ohio. Quality habitat and increased rates of reproduction are attributed as reasons for high muskrat densities 3-5 years following a drawdown. As emergent vegetation begins to senesce (van der Valk 2000) and muskrat densities become higher, reproductive rates drop (Beer and Truax1950, Errington 1961, Kroll and Meeks 1985, Clark 2000), and therefore muskrat populations tend to drop. It should be noted though that my analysis indicates that positive effects persist 5-9 years following a drawdown although the number of basins for comparison is small.

Muskrat densities did not differ in basins upstream or downstream of The Pas from 1980-1989. The perception of local resource users that the upper end of the delta is more productive may be biased for two reasons. First the upper end of the delta is closer to The Pas and has road access, making the RR and CRT complexes more accessible to resource users compared to SMC wetlands which have no road access and are >20 km from The Pas. Therefore, wetlands in the SMC are visited less frequently by resource users (Cross, Manitoba Conservation, personal comm.) making actual muskrat densities in the remote lower delta poorly understood by resource users. Secondly, wetland basins in RR and CRT complexes are larger (Appendix C Table 1), and, consequently, support larger muskrat populations, although the densities are similar to SMC wetlands. Therefore, a hypothetical doubling of muskrat populations in the larger basins upstream of The Pas, has a greater impact on total muskrat abundance, which may make these basins appear more productive, but may not affect house density. For example, a doubling in abundance from 1000 muskrats to 2000 in a 1000 ha basin, appears larger than an increase from 10 to 20 in a 10 ha basin, although the rate of change in density is the same. No difference in muskrat production between the upper and lower delta is a logical finding since the water level management practices between the upper and lower deltas during the time of study were similar.

Temperature and snow depth are presumed to affect muskrat survival, and therefore density (Jelinski 1989, Messier et al. 1990, Clark 1994, Toner et al. 2010). Increased snow depth in the SRD positively affected muskrat house densities. This is consistent with the findings Jelinski (1989), Messier et al. (1990) and Clark (1994) who found that snow trapped along steep river banks and or wetland vegetation decreased ice thickness allowing muskrats access to plant rhizomes.

Toner et al. (2010) found an interaction between water depth and overwinter temperature so that as water depth and overwinter temperature decreased, so did muskrat house abundance. I found no significant effects of temperature on muskrat houses density and did not explicitly measure water depth. I attempted to compensate for differences in depth by comparing the deeper wetlands in the upper delta to shallower wetlands in the lower delta. Although my model which included an interaction of location and temperature gained little support, it suggests that low temperatures affected densities in the shallower SMC wetlands more so than in the deeper wetlands in the upper delta. It may be that muskrat populations in the shallow SMC wetlands were more sensitive to the effects of temperature because deep water habitat for refuge from harsh overwinter conditions is limited in comparison to basins in the upper delta.

Both depth and vegetation are important habitat variables affecting habitat selection of muskrats (Erb and Perry 2003), but were not included in my model. Remote sensing and GIS technologies have made acquiring accurate and precise depth and vegetation (Gilmore et al. 2008) data cheaper and more precise than was available when these data were collected. Further study into the long term affects of water level manipulation on muskrat populations could include these variables in addition to the other variables in my model.

Water level manipulation is the primary muskrat technique (Erb and Perry 2003), and this analysis confirms that water level manipulation positively affects muskrats in the years after a drawdown. If a primary goal of water level manipulation is to increase muskrat production, then managers should consider the following recommendations (1) there is a tradeoff regarding the duration of a drawdown, longer drawdowns may confer greater benefits upon reflooding through nutrient cycling and vegetative regeneration, however long term average muskrat densities are reduced during the years of the drawdown. (2) Partial and complete drawdowns confer similar benefits to muskrat populations. Partial drawdowns are preferred because they leave refugia in the deep portions of the managed basins during the years of a drawdown that support muskrat densities similar to that of wetlands kept at full supply level (FSL) (Ervin 2011). In addition, partial drawdowns do not reduce the amount of open water in a basin (Baschuk 2010, Ervin 2011), are more attractive to waterfowl than wetlands kept at FSL (Baschuk 2010), and are cheaper and more logistically practical to implement than complete drawdowns. (3) If increased vegetation is needed, water levels should be managed to promote the growth of *Typha spp.* (Kroll and Meeks 1985) and *Equisetum spp.* (Jelinski 1989, Ervin 2011). (4) Wetlands could be drawndown in approximately 4-6 year cycles that will allow muskrat populations to respond to a drawdown and maintain long term density.

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CHAPTER 5: GENERAL CONCLUSION

Hydroelectric developments have significantly altered the hydrology and the historical wetland cycle in the SRD by reducing both long term and within year flood frequency. Over bank flood frequencies are predicted to be reduced from one in ten years to one in fifty years. Reductions in flood frequencies and the impoundment of water in SRD wetlands will continue to alter the natural ebb and flow in these deltaic wetlands. Although Ducks Unlimited Canada (DUC) has attempted to manage the SMC wetlands for muskrat and waterfowl production through water level manipulation financial, logistical, and regulatory restrictions have made intense management difficult. Ultimately, changes in muskrat populations are related to the large scale, long term factors largely beyond the control of small scale management. However, this research shows that water level drawdowns are effective means of stimulating muskrat populations. The research details the responses of the wetlands to water level manipulation and links it to the habitats selected by muskrats thus highlighting the conditions that should be the focus of wetland management.

Following the partial drawdown in the fall of 2007, muskrat densities derived from mark recapture surveys did not differ between PD and FSL wetlands. Although muskrat populations usually briefly fall following drawdowns due to a reduced amount of habitat, in the SMC they were not did not eliminated in the PD wetlands. On a per flooded area basis, PD wetland supported residual muskrat population at similar densities as FSL wetlands during the years of the drawdown. Higher N/L quotient sin PD wetlands may indicate some potential physiological stress of the drawdown, although other condition indices did not differ in PD and FSL wetlands.

The partial drawdown resulted in increased amounts of senescent vegetation in PD wetlands in 2008 and 2009, mainly affecting *Carex* and *Typha* vegetation classes. In the short term, the distribution of open water and other vegetation classes were unaffected by the water level reduction. The responses of the vegetation communities in SMC wetlands to water level manipulation differed from that of well-studied prairie wetlands systems, displaying indistinct zonation patterns and increased flooding depth tolerances. Studies on the development of depth tolerances, the formation of floating vegetation , and the role of frozen substrates would be important contributions to fully understanding the impacts of water level manipulation on the SMC wetlands.

The result of habitat selection modeling was generally consistent with other studies of muskrats, although it was complicated by the habitat structure of these northern wetlands. Muskrats selected for rooted *Typha* with greater frequency than any other habitat, followed by rooted *Equisetum.* In general muskrats selected for house location in rooted habitats over floating habitats. Active house locations were positively correlated with distance to upland and depth, and negatively correlated with distance to open water and a vegetation robustness index, greenness. As in other studies, *Typha spp.* was a preferred habitat and food, with the lowest ADF content and the highest CP content. The partial drawdown had no general effect on ADF or CP of all species groups but individual species responded to the drawdown .

DUC's records from 1979 to 1990 show that water level drawdowns were successful at increasing muskrat house densities in SRD wetlands. In the years after a drawdown muskrat house densities generally increased and peaked three years after a drawdown, however the ten year densities were unaffected. Partial and complete drawdowns had similar effects on muskrat densities compared to no drawdown, but the responses to management were variable among wetlands. Snow depth and muskrat house densities were positively correlated, however temperature and location relative to The Pas had no effect on muskrat house densities. Depending on objective and resources, this research provides guidance on the duration of drawdowns, the effects of partial or complete drawdown, and the intervals between drawdowns that will enhance muskrat populations in SMC wetlands.

Low muskrat densities, and low recruitment in SMC wetlands compared to other northern deltas are likely due to degenerating wetland habitat conditions created by prolonged water level stabilization. The highest muskrat densities in the SRD, reported in historical records dating back to the 1930's occurred in the decade following the drought of the 1930's. Upon reflooding of the wetlands by higher river water level, and impoundment by newly constructed water control structures, high quality habitat was abundant and muskrat populations boomed (McLeod 1950). This large scale completion of the wetland cycle was responsible for supporting the largest muskrat populations on record, and has not been mimicked in scale since.

Smaller scale water level manipulation efforts by various managers, most notably Ducks Unlimited Canada, have produced similar increases in muskrat populations, though not as obvious because of their lesser extent. Over the years water level management in the SMC has varied but the combination of relatively high water and restricted management practices has promoted the current degenerating wetland conditions. Although expensive and logistically difficult the results I have presented suggest that a large scale drawdown and refill would stimulate muskrat populations in the SMC and more generally the entire SRD.

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APPENDIX A: WATER LEVELS IN THE SUMMERBERRY MARSH COMPLEX STUDY WETLANDS 1997-2009

Figures 1-6 show the water levels in Summerberry marsh Complex study wetlands from 1997-2009. Prior to an over bank flood event of the Saskatchewan River in 2005 all study wetlands were below full supply level. Interestingly wetland 35HI had the lowest water levels before 2005, supported the highest muskrat abundances of any PD during the study, and had the highest number of captures in the September 2009 sampling period. I speculate that this is evidence of the benefit to muskrat populations of a drawdown refill cycle, and also evidence that the magnitude of a drawdown (i.e. amount of water removed) also affects the responses of muskrat populations.

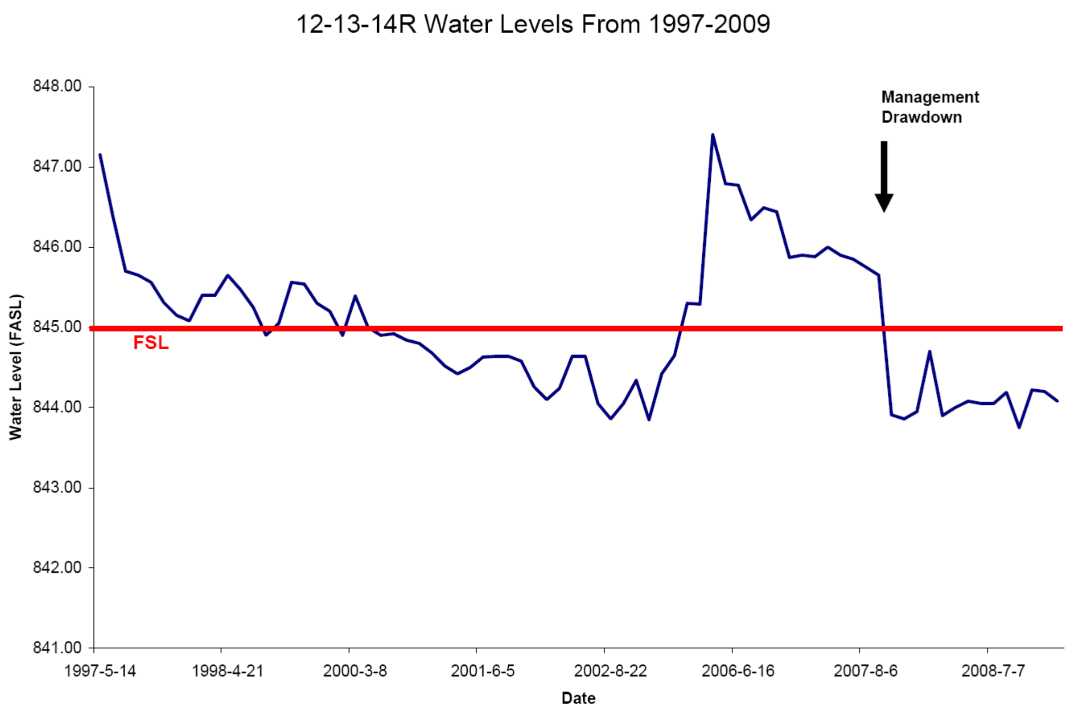


Fig. 1. Water levels in feet above sea level (FASL) in wetland 14R, a partial drawdown wetland, at the Summerberry Marsh Complex, The Pas, Manitoba, Canada from 1997-2009.

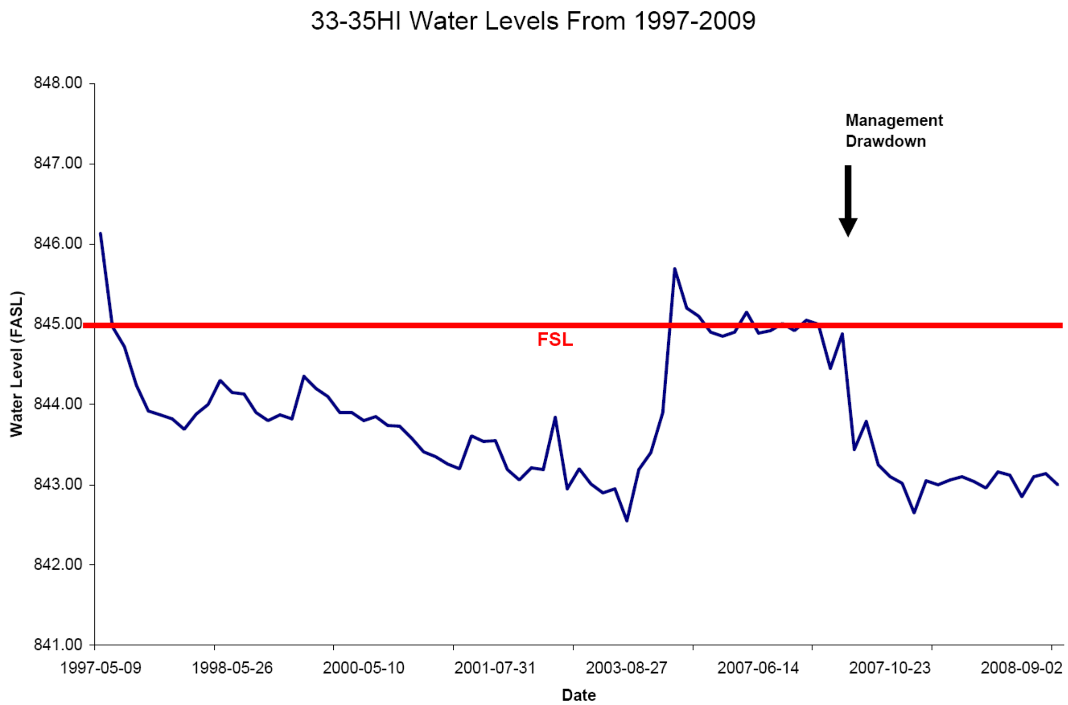


Fig. 2. Water levels in feet above sea level (FASL) in wetland 35HI, a partial drawdown wetland, at the Summerberry Marsh Complex, The Pas, Manitoba, Canada from 1997-2009.

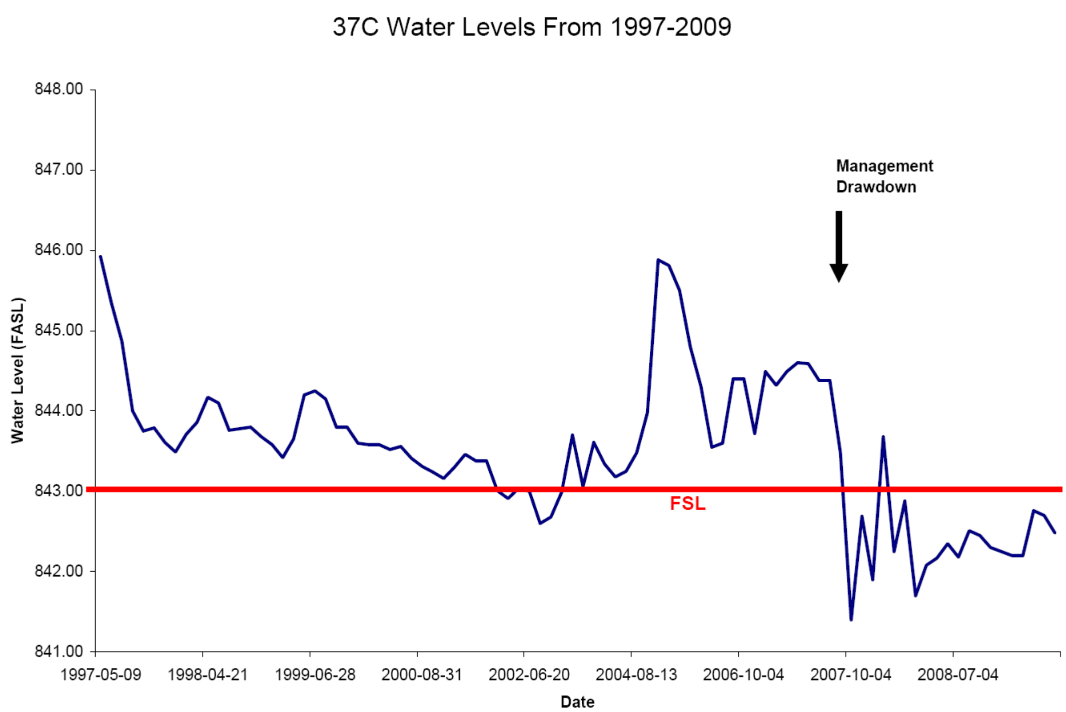


Fig. 3. Water levels in feet above sea level (FASL) in wetland 37C, a partial drawdown wetland, at the Summerberry Marsh Complex, The Pas, Manitoba, Canada from 1997-2009.

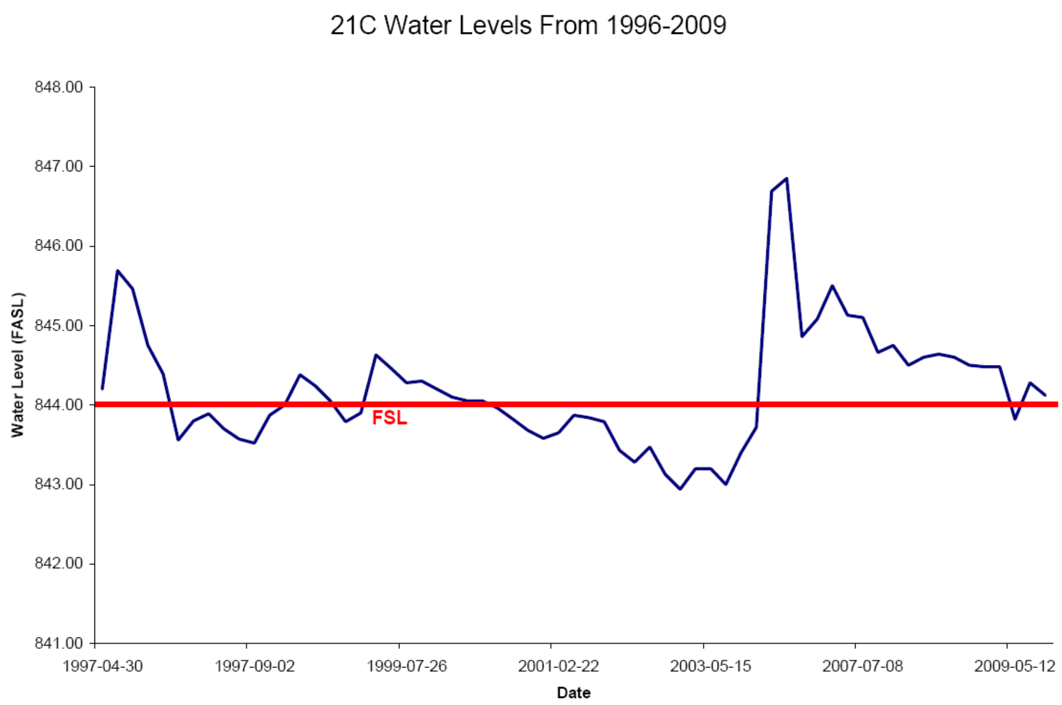


Fig. 4. Water levels in feet above sea level (FASL) in wetland 21C, a full supply level wetland, at the Summerberry Marsh Complex, The Pas, Manitoba, Canada from 1997-2009.

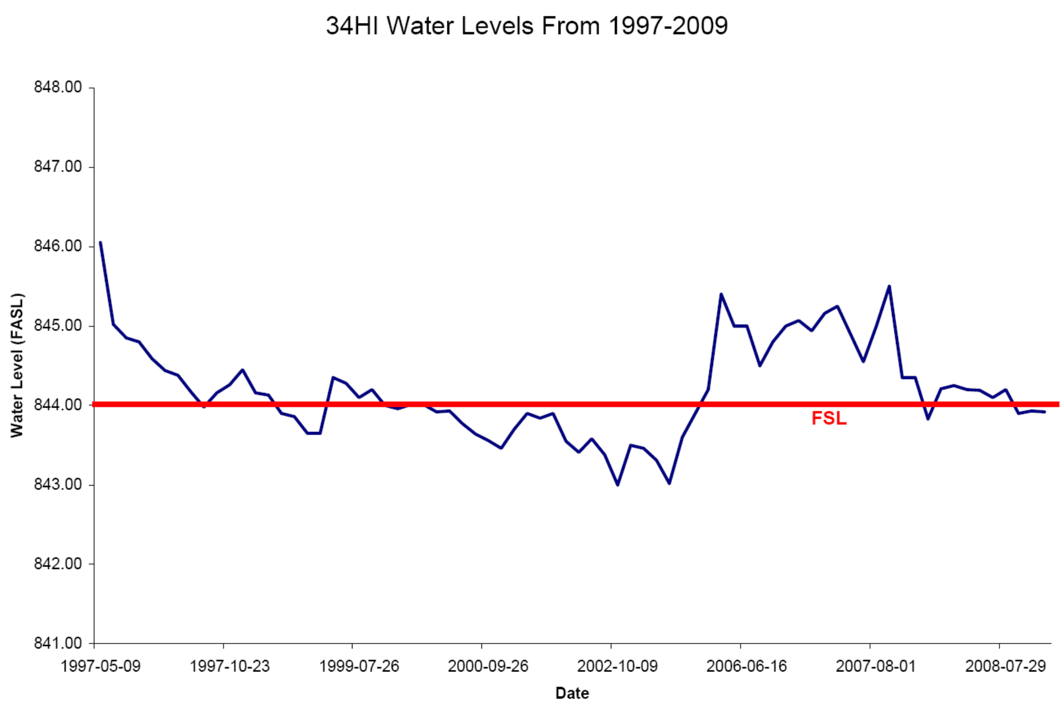


Fig. 5. Water levels in feet above sea level (FASL) in wetland 34HI, a full supply level wetland, at the Summerberry Marsh Complex, The Pas, Manitoba, Canada from 1997-2009.

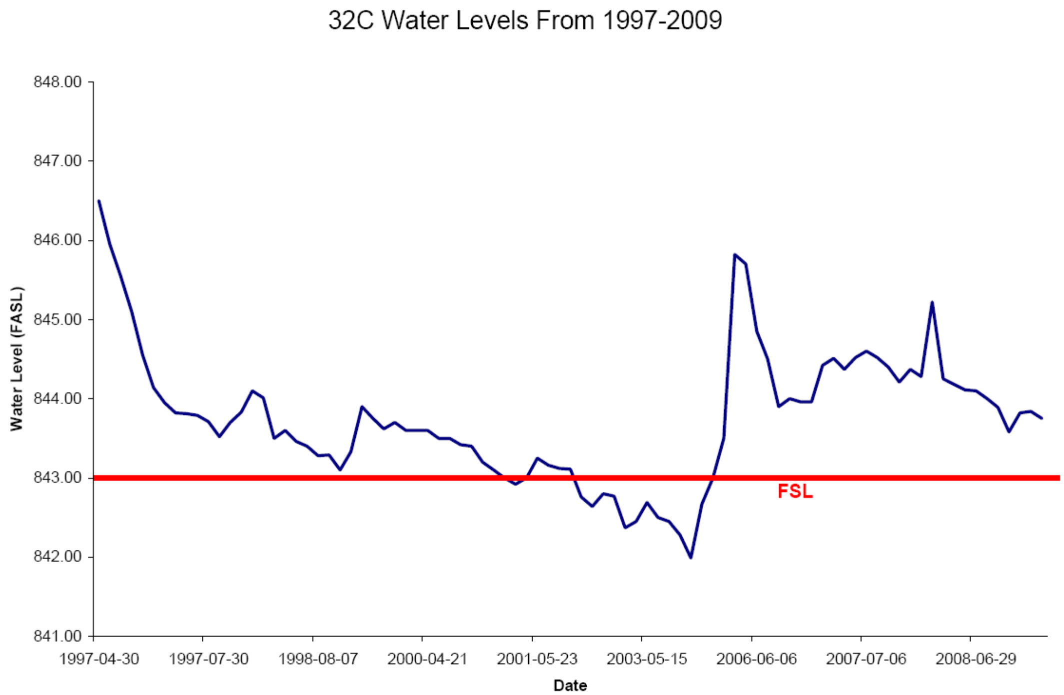


Fig. 6. Water levels in feet above sea level (FASL) in wetland 32C, a full supply level wetland, at the Summerberry Marsh Complex, The Pas, Manitoba, Canada from 1997-2009.

APPENDIX B: CLASSIFICATION OF WETLAND VEGETATION AT THE SUMMERBERRY MARSH COMPLEX, THE PAS, MANITOBA, CANADA FOLLOWING A WATER LEVEL MANIPULATION OF 30CM USING OBJECT ORIENTED CLASSIFICATION METHODS

Methods

Water Level Manipulation

Each of the six study wetland has a water control structure to facilitate water level manipulation and control. Water level manipulation began in the spring of 2007. Partial drawdowns, to approximately 30 cm below full supply level, were implemented on the three 'partial drawdown (PD)' wetlands; 14R, 35HI, and 37C. The remaining three 'full supply level (FSL)' wetlands, 21C, 34HI, and 32C, were held at approximately FSL and designated as experimental controls (Fig. 1). Wetlands remained at approximately these levels through 2010. Water levels were recorded weekly throughout the summer sampling periods, and data loggers recorded winter water levels, to ensure water remained at target levels (see Appendix A).

Results

The most accurate model in all cases except in PD wetlands in 2008 used backward parameter selection with SLSTAY set at $\alpha = .01$ (Table 1). In PD wetlands in 2008 stepwise parameter selection produced the most accurate model. The standard deviation of the NIR band, NDVI, mean NIR, mean green, mean blue, and depth covariates were always included in the most accurate model (Table 2).

The partial drawdown resulted in an increased amount of senescent vegetation in PD wetlands in 2008 and 2009. *Carex* and *Typha* were negatively affected by the partial drawdown, and contributed to most the increase in senescent vegetation. The remaining species classes showed little change in both PD and FSL wetlands, and the proportion of open water did not change in PD or FSL wetlands from 2007-2009 (Fig. 2-8).

Overall prediction accuracy was high (Tables 3 and 4). The senescent vegetation class was consistently predicted with the highest accuracy ranging from 90-99% and averaging 96.6% among PD and FSL wetlands and all years. The *Typha spp.* class was predicted with the lowest accuracy ranging from 52-65% and averaging 62.0% among PD and FSL wetlands and all years. Trees, Water, *Scirpus spp.*, *Carex spp.*, *Phragmites spp.*, and *Equisetum spp.* classes were predicted in order from second highest to second lowest prediction accuracy. Prediction accuracies are presented for each wetland and year in Figures 9-14.

Prediction probability matrices are presented in Tables 3 and 4, and in Figs. 5-10. In each row for a given vegetation class, the column that corresponds with the same vegetation class represents the proportion of polygons ground truthed as that vegetation type and correctly predicted by the logistic regression model. Therefore, the proportions of each vegetation type correctly predicted appear along the diagonals of each matrix (in bold face in Tables, and in yellow in Figs.) In addition, along each row, a proportion is presented for each of the other vegetation classes, and represents the proportion of polygons which were ground truthed as the vegetation type labeled in that row, but predicted as the vegetation type labeled in the corresponding column. Conversely down each column proportions are presented which represent polygons ground truthed as a vegetation type other than the column label, but predicted by the model as the vegetation type in the column label.

Table 1: Parameters retained in the most accurate logistic regression models used classify wetland vegetation following a water level drawdown at the Summerberry Marsh Complex, The Pas, Manitoba, Canada from 2007-2009.

	Year					
	2007		**2008**		**2009**	
Parameter	**FSL**	**PD**	**FSL**	**PD**	**FSL**	**PD**
NDVI	*	*	*	*	*	*
mean_Blue	*	*	*	*	*	*
mean_Green	*	*	*	*	*	*
mean_NIR	*	*	*	*	*	*
Depth	*	*	*	*	*	*
NIR_Std Dev	*	*	*	*	*	*
mean_Red	*	*	*	*	*	
Blue_Std Dev	*	*	*		*	*
GNDVI	*	*		*	*	
Red_Std Dev	*		*		*	*
Max_diff		*	*		*	*
Green_Std Dev		*			*	*
Brightness			*	*		

* - indicates the parameter was retained in the most accurately predicting models

Table 2: Vegetation classification prediction probabilities, predicted average depth (cm) per class, and predicted total area (ha) per class for full supply level (FSL) wetlands classified using logistic regression at the Summerberry Marsh Complex, The Pas, Manitoba, Canada, 2007-2009.

FSL 2007	**Prediction Probability Matrix**								**Species Class Characteristics**	
Class	**Carex**	**Senescent**	**Equisetum**	**Phragmites**	**Scirpus**	**Trees**	**Typha**	**Water**	**Ave Depth (cm)**	**Total Area (ha)**
Carex	**0.7039**	0.0110	0.0871	0.0986	0.0000	0.0675	0.0280	0.0038	28.8396	98.6317
Senescent	0.0162	**0.9686**	0.0009	0.0021	0.0000	0.0044	0.0059	0.0019	44.4745	38.6307
Equisetum	0.1544	0.0007	**0.6929**	0.0844	0.0060	0.0299	0.0265	0.0051	33.4787	41.3968
Phragmites	0.0481	0.0001	0.0240	**0.7381**	0.0177	0.0030	0.1229	0.0461	82.9637	156.0869
Scirpus	0.0005	0.0000	0.0168	0.0740	**0.7637**	0.0001	0.1071	0.0378	95.1475	48.2181
Trees	0.1076	0.0026	0.0320	0.0209	0.0000	**0.8312**	0.0042	0.0014	12.6326	40.0388
Typha	0.0383	0.0096	0.0224	0.1644	0.0517	0.0011	**0.6794**	0.0331	91.7492	22.0138
Water	0.0014	0.0000	0.0066	0.1101	0.0622	0.0004	0.0512	**0.7681**	92.1632	77.8677
FSL 2008	**Prediction Probability Matrix**								**Species Class Characteristics**	
Class	**Carex**	**Senescent**	**Equisetum**	**Phragmites**	**Scirpus**	**Trees**	**Typha**	**Water**	**Ave Depth (cm)**	**Total Area (ha)**
Carex	**0.7530**	0.0001	0.0782	0.0921	0.0003	0.0410	0.0335	0.0018	30.0365	106.0635
Senescent	0.0001	**0.9840**	0.0000	0.0029	0.0012	0.0000	0.0097	0.0020	69.6878	10.0351
Equisetum	0.0944	0.0000	**0.7285**	0.0983	0.0026	0.0420	0.0170	0.0171	37.1003	43.4302
Phragmites	0.0333	0.0003	0.0380	**0.7767**	0.0122	0.0048	0.0704	0.0641	76.5077	140.1042
Scirpus	0.0000	0.0000	0.0049	0.0412	**0.7251**	0.0000	0.1100	0.1187	93.7247	49.3494
Trees	0.0355	0.0000	0.0320	0.0165	0.0000	**0.9151**	0.0003	0.0004	9.1591	62.0496
Typha	0.0439	0.0040	0.0116	0.1682	0.0834	0.0000	**0.6411**	0.0478	79.2568	41.1438
Water	0.0003	0.0008	0.0174	0.0891	0.0863	0.0004	0.0385	**0.7672**	87.4947	70.6646
FSL 2009	**Prediction Probability Matrix**								**Species Class Characteristics**	
Class	**Carex**	**Senescent**	**Equisetum**	**Phragmites**	**Scirpus**	**Trees**	**Typha**	**Water**	**Ave Depth (cm)**	**Total Area (ha)**
Carex	**0.8103**	0.0031	0.0631	0.0854	0.0002	0.0136	0.0190	0.0052	29.1687	70.9044
Senescent	0.0040	**0.9910**	0.0010	0.0012	0.0000	0.0000	0.0019	0.0009	53.5969	57.9533
Equisetum	0.1012	0.0012	**0.7472**	0.0649	0.0046	0.0574	0.0197	0.0037	32.5849	44.1765
Phragmites	0.0445	0.0003	0.0223	**0.7651**	0.0314	0.0002	0.0755	0.0607	79.0996	139.1520
Scirpus	0.0008	0.0000	0.0091	0.0665	**0.8068**	0.0000	0.0718	0.0450	94.0178	48.7995
Trees	0.0154	0.0000	0.0517	0.0024	0.0000	**0.9298**	0.0000	0.0006	7.6891	56.7932
Typha	0.0349	0.0029	0.0316	0.1766	0.0709	0.0000	**0.6493**	0.0337	79.5264	27.2902
Water	0.0046	0.0004	0.0025	0.1044	0.0376	0.0003	0.0320	**0.8182**	81.3731	77.7623

*** bold text indicates percent accuracy per vegetation class**

Table 3: Vegetation classification prediction probabilities, average depth (cm) per class, and total area (ha) per class for partial drawdown (PD) wetlands classified using logistic regression at the Summerberry Marsh Complex, The Pas, Manitoba, Canada, 2007-2009.

PD 2007	**Prediction Probability Matrix**								**Species Class Characteristics**	
Class	**Carex**	**Senescent**	**Equisetum**	**Phragmites**	**Scirpus**	**Trees**	**Typha**	**Water**	**Ave Depth (cm)**	**Total Area (ha)**
Carex	**0.7331**	0.0044	0.0464	0.1475	0.0011	0.0086	0.0571	0.0017	45.5340	207.5630
Senescent	0.0212	**0.8972**	0.0049	0.0304	0.0067	0.0053	0.0333	0.0010	82.3014	44.6574
Equisetum	0.1859	0.0032	**0.5801**	0.1052	0.0051	0.0017	0.1155	0.0033	56.1408	16.8346
Phragmites	0.1658	0.0083	0.0454	**0.5790**	0.0153	0.0030	0.1693	0.0138	85.3518	79.6143
Scirpus	0.0068	0.0066	0.0056	0.0373	**0.7846**	0.0001	0.1308	0.0282	111.9485	27.9577
Trees	0.0236	0.0105	0.0018	0.0117	0.0000	**0.9479**	0.0045	0.0000	20.7732	47.3051
Typha	0.0684	0.0155	0.0363	0.1715	0.0512	0.0016	**0.6462**	0.0093	91.6840	101.0818
Water	0.0261	0.0004	0.0060	0.0379	0.0575	0.0001	0.0316	**0.8404**	112.0148	91.9124

PD 2008	**Prediction Probability Matrix**								**Species Class Characteristics**	
Class	**Carex**	**Senescent**	**Equisetum**	**Phragmites**	**Scirpus**	**Trees**	**Typha**	**Water**	**Ave Depth (cm)**	**Total Area (ha)**
Carex	**0.7496**	0.0032	0.0549	0.1230	0.0048	0.0103	0.0353	0.0190	7.5279	133.2882
Senescent	0.0051	**0.9724**	0.0010	0.0047	0.0052	0.0000	0.0112	0.0003	25.7134	184.2005
Equisetum	0.1408	0.0000	**0.6115**	0.1340	0.0062	0.0684	0.0153	0.0237	12.2104	12.2621
Phragmites	0.1288	0.0027	0.0527	**0.6191**	0.0328	0.0087	0.1320	0.0231	30.7147	86.6956
Scirpus	0.0186	0.0055	0.0056	0.0521	**0.7360**	0.0003	0.1204	0.0614	51.2521	33.0302
Trees	0.0155	0.0000	0.0226	0.0121	0.0001	**0.9472**	0.0013	0.0010	6.5437	54.6835
Typha	0.0920	0.0263	0.0346	0.1297	0.1107	0.0003	**0.5831**	0.0233	38.8287	27.6817
Water	0.0523	0.0004	0.0097	0.0325	0.0498	0.0008	0.0209	**0.8335**	51.7114	85.3434

PD 2009	**Prediction Probability Matrix**								**Species Class Characteristics**	
Class	**Carex**	**Senescent**	**Equisetum**	**Phragmites**	**Scirpus**	**Trees**	**Typha**	**Water**	**Ave Depth (cm)**	**Total Area (ha)**
Carex	**0.6925**	0.0146	0.0576	0.1321	0.0047	0.0228	0.0659	0.0097	13.4914	44.1516
Senescent	0.0032	**0.9914**	0.0002	0.0026	0.0009	0.0001	0.0012	0.0002	23.1466	277.5343
Equisetum	0.1499	0.0000	**0.5641**	0.1244	0.0484	0.0220	0.0584	0.0327	26.1178	7.1114
Phragmites	0.1014	0.0054	0.0398	**0.6430**	0.0834	0.0011	0.1038	0.0220	34.7675	67.2048
Scirpus	0.0151	0.0038	0.0232	0.1069	**0.7575**	0.0012	0.0458	0.0464	50.7257	36.3935
Trees	0.0121	0.0005	0.0047	0.0030	0.0005	**0.9775**	0.0010	0.0007	5.8924	89.8593
Typha	0.1276	0.0038	0.0423	0.1860	0.0900	0.0023	**0.5183**	0.0297	42.6658	8.1631
Water	0.0313	0.0003	0.0116	0.0313	0.0375	0.0017	0.0177	**0.8685**	49.2589	86.7968

*** bold text indicates percent accuracy per vegetation class**

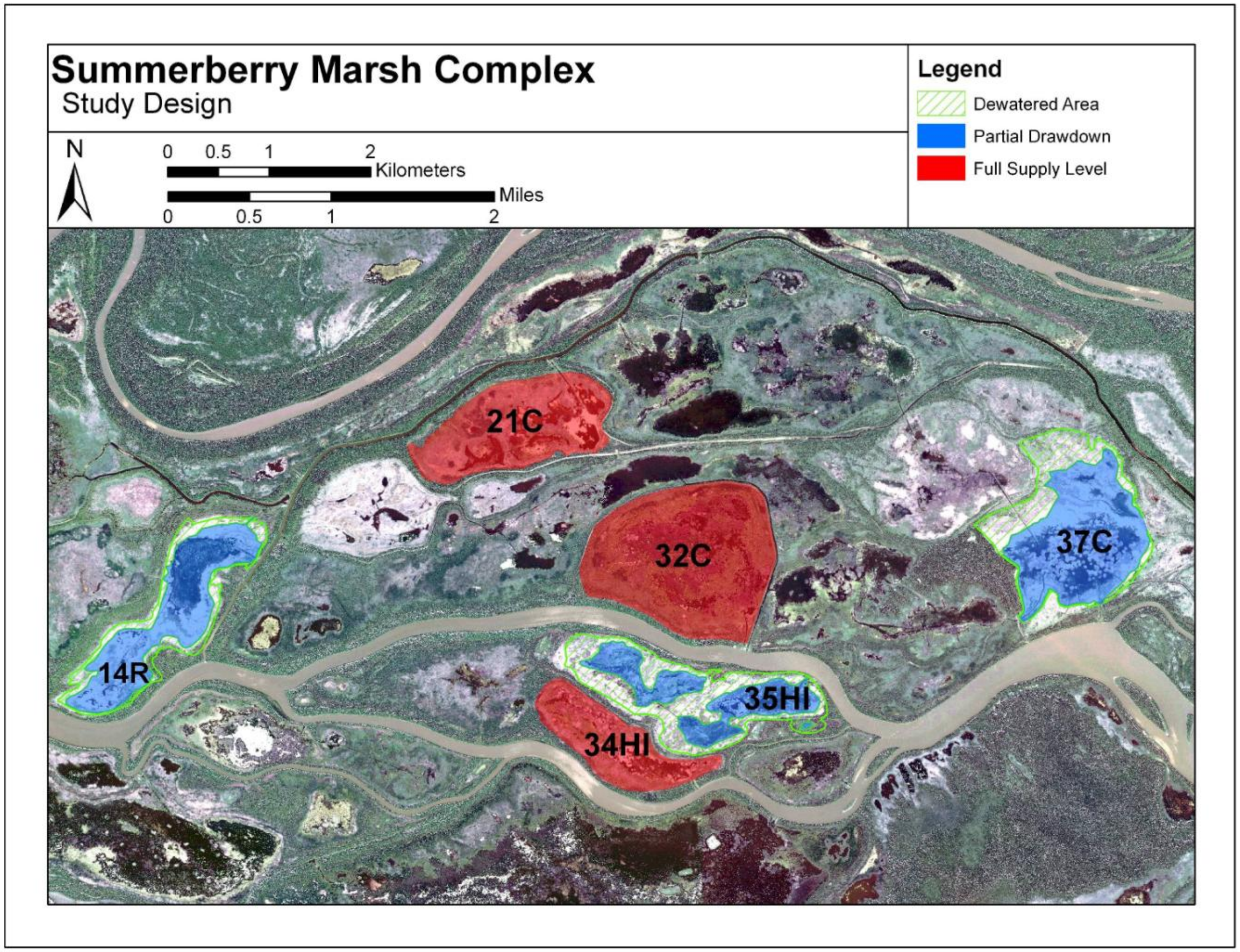


Fig. 1. Study design displaying FSL and PD wetlands, as well as the area dewatered by the partial drawdown, at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

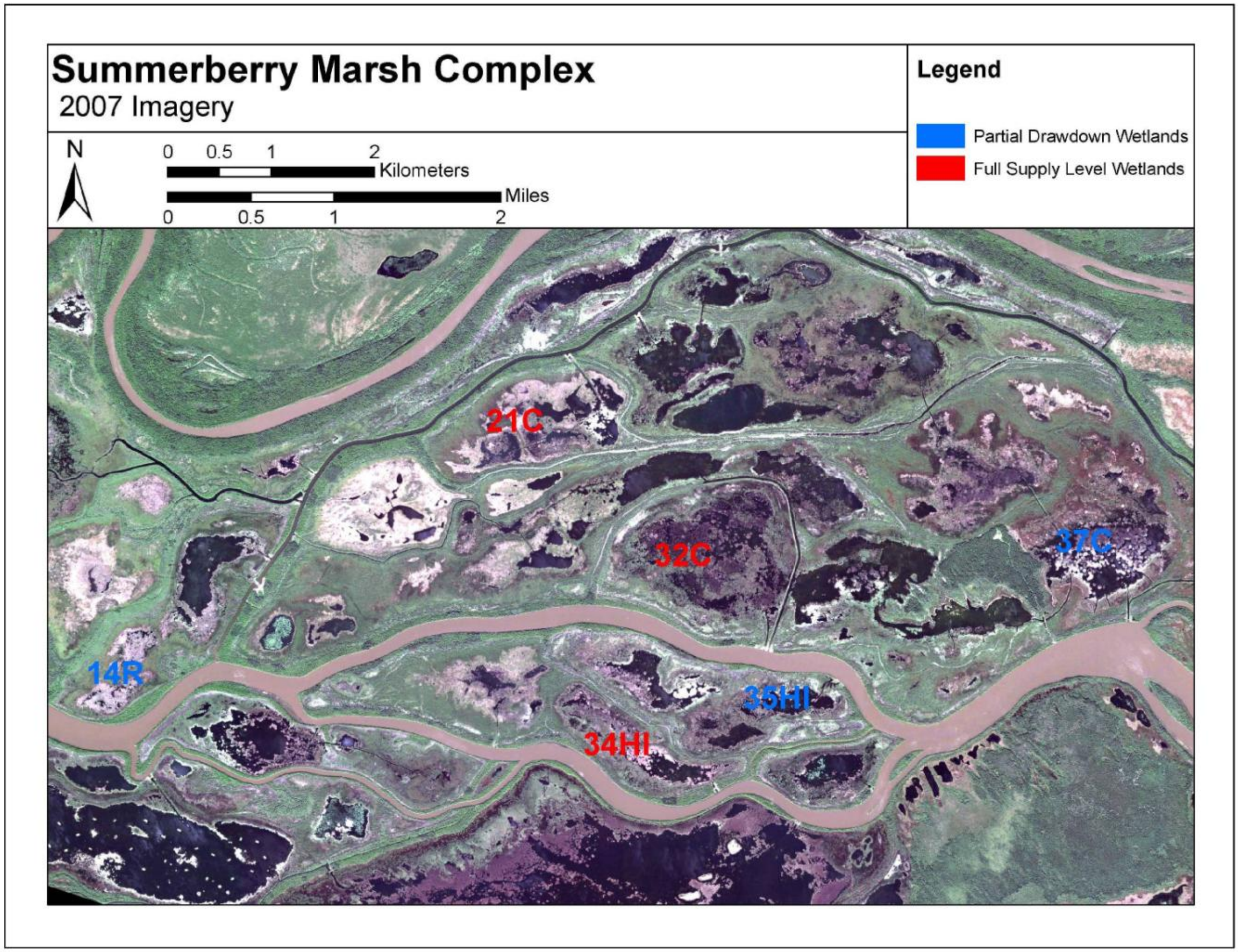


Fig. 2. Quickbird® imagery taken on 27 June 2007 before the partial drawdown, at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

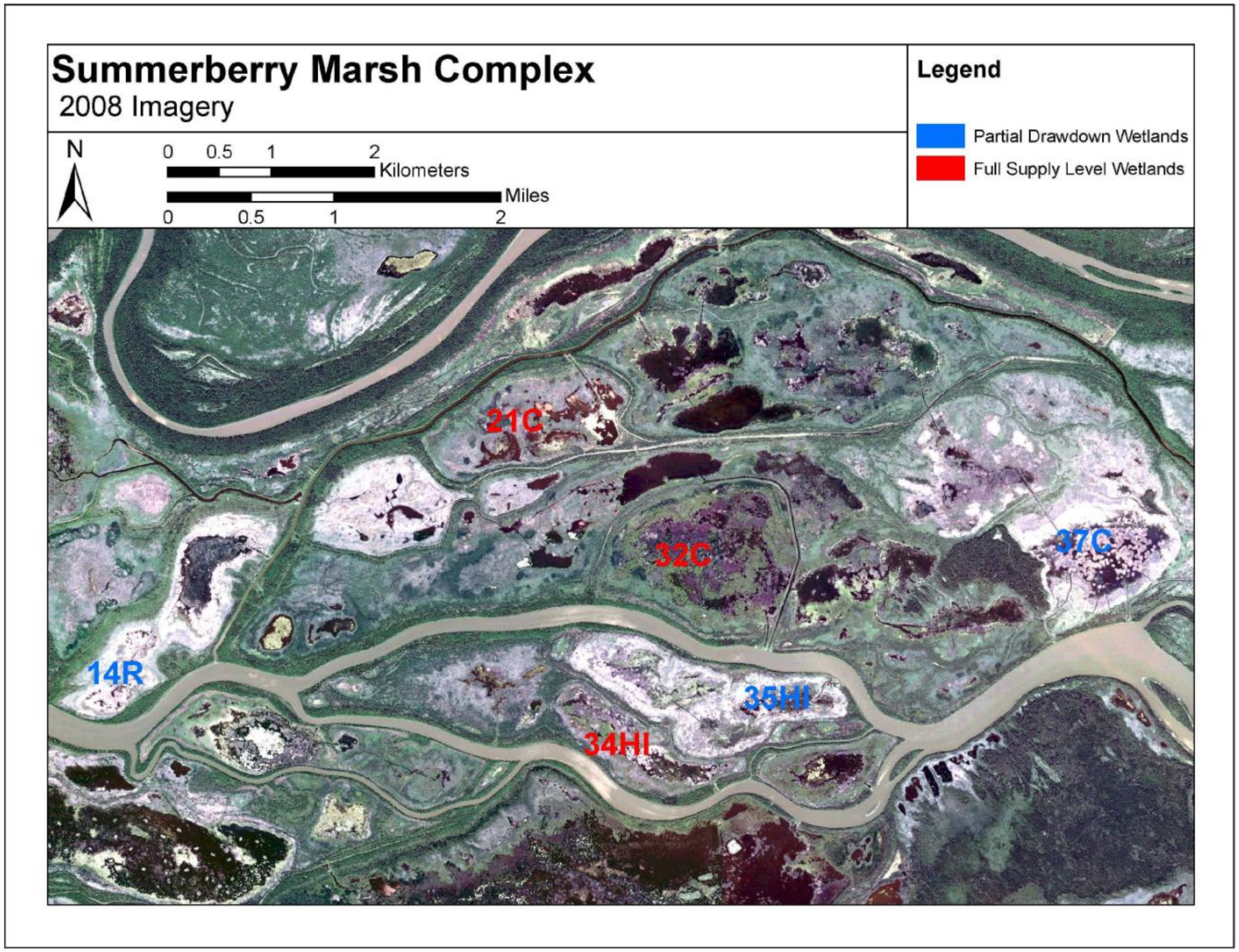


Fig. 3. Quickbird® imagery taken on 4 July 2008, the summer following the partial drawdown, at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

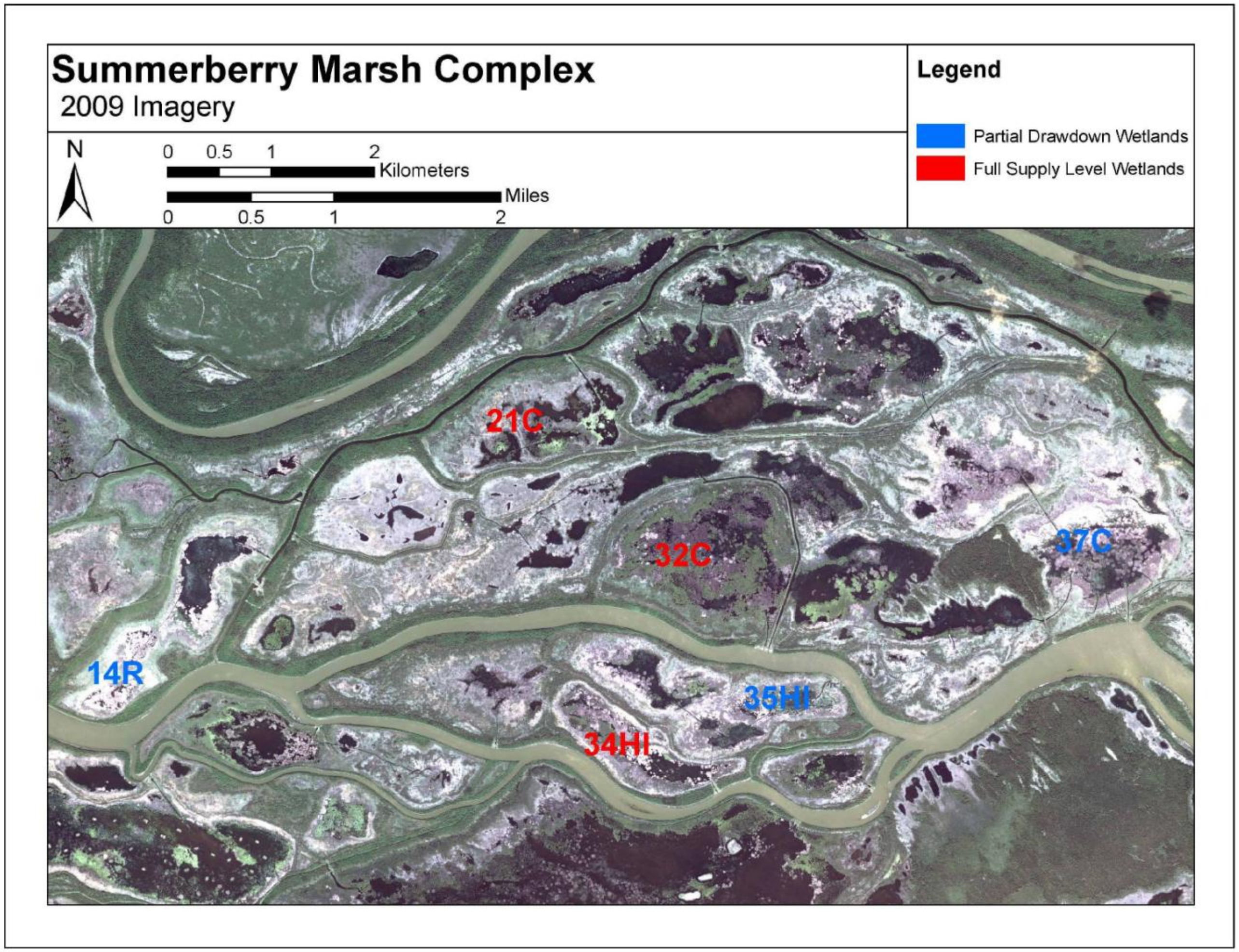
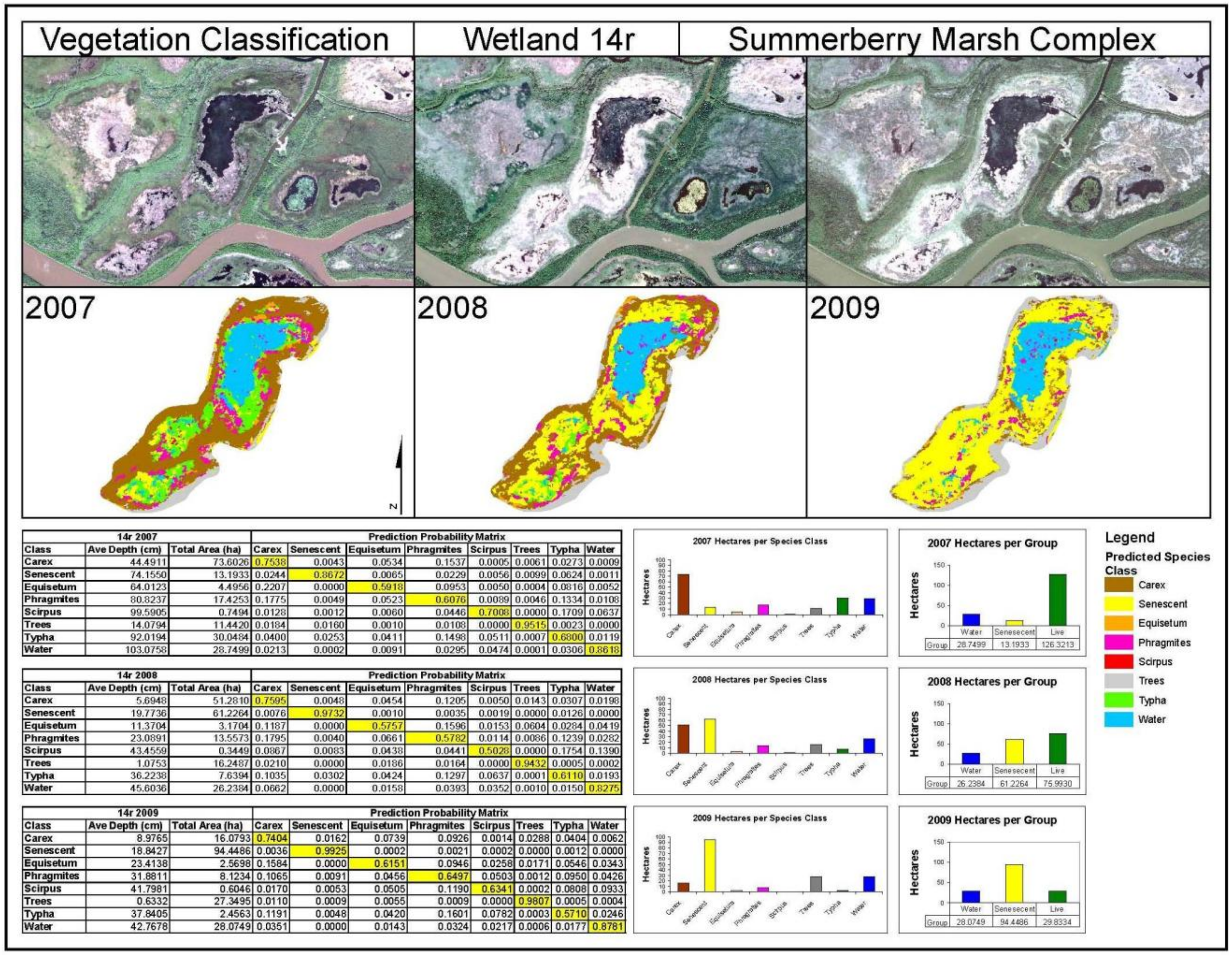


Fig. 4. Quickbird® imagery taken on 7 July 2009, two summers following the partial drawdown, at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

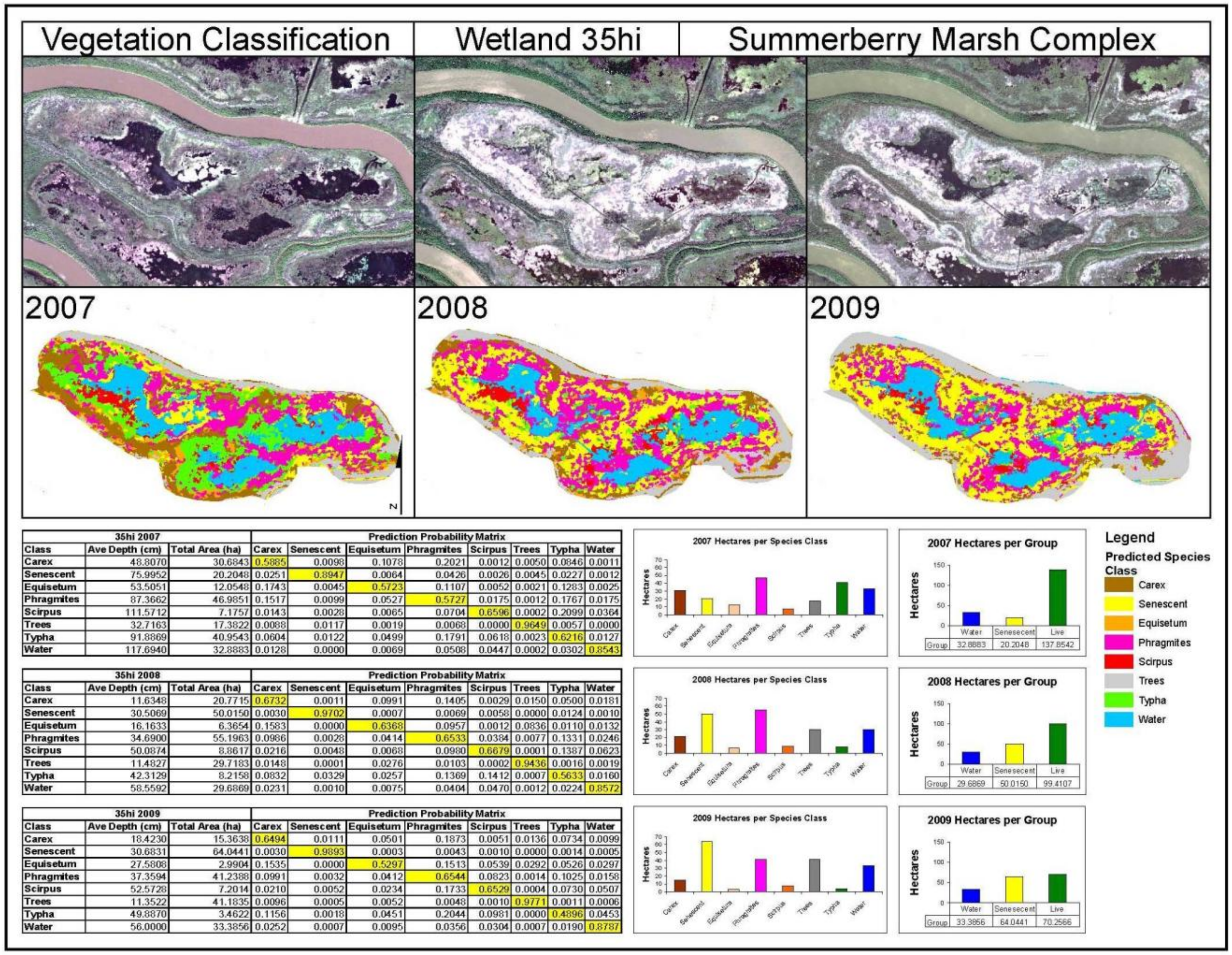


14r 2007			Prediction Probability Matrix							
Class	Ave Depth (cm)	Total Area (ha)	Carex	Senescent	Equisetum	Phragmites	Scirpus	Trees	Typha	Water
Carex	44.4911	73.6026	0.7538	0.0043	0.0534	0.1537	0.0005	0.0061	0.0273	0.0009
Senescent	74.1550	13.1933	0.0244	0.8672	0.0065	0.0229	0.0056	0.0099	0.0624	0.0011
Equisetum	64.0123	4.4956	0.2207	0.0000	0.5918	0.0953	0.0050	0.0004	0.0816	0.0052
Phragmites	80.8237	17.4253	0.1775	0.0049	0.0523	0.6076	0.0089	0.0046	0.1334	0.0108
Scirpus	99.5905	0.7494	0.0128	0.0012	0.0060	0.0446	0.7008	0.0000	0.1709	0.0637
Trees	14.0794	11.4420	0.0184	0.0160	0.0010	0.0108	0.0000	0.9515	0.0023	0.0000
Typha	92.0194	30.0484	0.0400	0.0253	0.0411	0.1498	0.0511	0.0007	0.6800	0.0119
Water	103.0758	28.7499	0.0213	0.0002	0.0091	0.0295	0.0474	0.0001	0.0306	0.8618

14r 2008			Prediction Probability Matrix							
Class	Ave Depth (cm)	Total Area (ha)	Carex	Senescent	Equisetum	Phragmites	Scirpus	Trees	Typha	Water
Carex	5.6948	51.2810	0.7595	0.0048	0.0454	0.1205	0.0050	0.0143	0.0307	0.0198
Senescent	19.7736	61.2264	0.0076	0.9732	0.0010	0.0035	0.0019	0.0000	0.0126	0.0000
Equisetum	11.3704	3.1704	0.1187	0.0000	0.5757	0.1596	0.0153	0.0604	0.0284	0.0419
Phragmites	23.0891	13.5573	0.1795	0.0040	0.0661	0.5782	0.0114	0.0086	0.1239	0.0282
Scirpus	43.4559	0.3449	0.0867	0.0083	0.0438	0.0441	0.5028	0.0000	0.1754	0.1390
Trees	1.0753	16.2487	0.0210	0.0000	0.0186	0.0164	0.0000	0.9432	0.0005	0.0002
Typha	36.2238	7.6394	0.1035	0.0302	0.0424	0.1297	0.0637	0.0001	0.6110	0.0193
Water	45.6036	26.2384	0.0662	0.0000	0.0158	0.0393	0.0352	0.0010	0.0150	0.8275

14r 2009			Prediction Probability Matrix							
Class	Ave Depth (cm)	Total Area (ha)	Carex	Senescent	Equisetum	Phragmites	Scirpus	Trees	Typha	Water
Carex	8.9765	16.0793	0.7404	0.0162	0.0739	0.0926	0.0014	0.0288	0.0404	0.0062
Senescent	18.8427	94.4486	0.0036	0.9925	0.0002	0.0021	0.0002	0.0000	0.0012	0.0000
Equisetum	23.4138	2.5698	0.1584	0.0000	0.6151	0.0946	0.0258	0.0171	0.0546	0.0343
Phragmites	31.8811	8.1234	0.1065	0.0091	0.0456	0.6497	0.0503	0.0012	0.0950	0.0426
Scirpus	41.7981	0.6046	0.0170	0.0053	0.0505	0.1190	0.6341	0.0002	0.0808	0.0933
Trees	0.6332	27.3495	0.0110	0.0009	0.0055	0.0009	0.0000	0.9807	0.0005	0.0004
Typha	37.8405	2.4563	0.1191	0.0048	0.0420	0.1601	0.0782	0.0003	0.5710	0.0246
Water	42.7678	28.0749	0.0351	0.0000	0.0143	0.0324	0.0217	0.0006	0.0177	0.8781

Fig. 5. Quickbird® imagery, vegetation classification, confusion matrices, species class changes over time in wetland 14r, a partial drawdown wetland, 2007-2009 at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

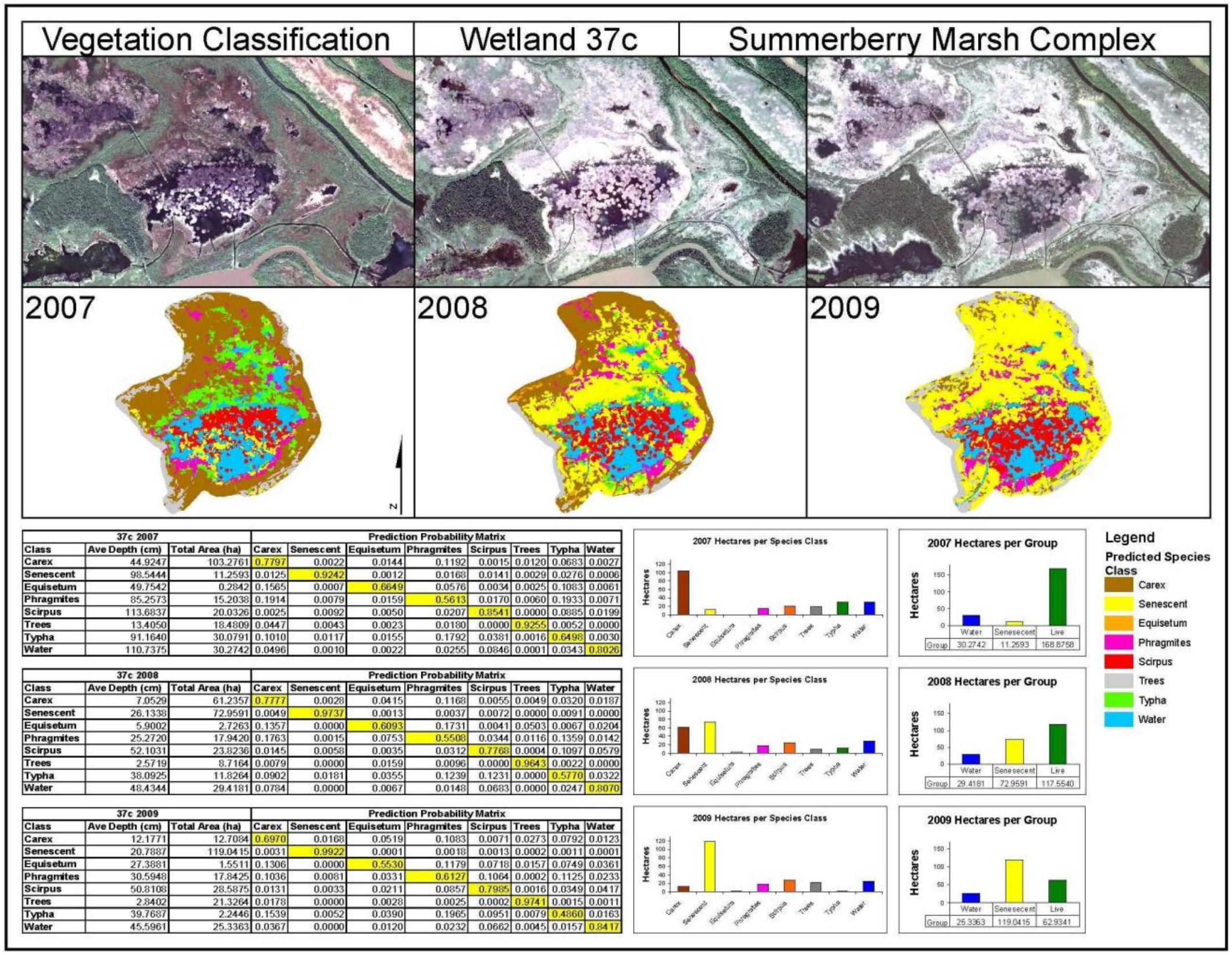


35hi 2007			Prediction Probability Matrix							
Class	Ave Depth (cm)	Total Area (ha)	Carex	Senescent	Equisetum	Phragmites	Scirpus	Trees	Typha	Water
Carex	48.8070	30.6843	0.5885	0.0098	0.1078	0.2021	0.0012	0.0050	0.0846	0.0011
Senescent	75.9952	20.2048	0.0251	0.8947	0.0064	0.0426	0.0026	0.0045	0.0227	0.0012
Equisetum	53.5051	12.0548	0.1743	0.0045	0.5723	0.1107	0.0052	0.0021	0.1283	0.0025
Phragmites	87.3662	46.9851	0.1517	0.0099	0.0527	0.5727	0.0175	0.0012	0.1767	0.0175
Scirpus	111.5712	7.1757	0.0143	0.0028	0.0065	0.0704	0.6596	0.0002	0.2099	0.0364
Trees	32.7163	17.3822	0.0088	0.0117	0.0019	0.0068	0.0000	0.9649	0.0057	0.0000
Typha	91.8869	40.9543	0.0604	0.0122	0.0499	0.1791	0.0618	0.0023	0.6216	0.0127
Water	117.6940	32.8883	0.0128	0.0000	0.0069	0.0508	0.0447	0.0002	0.0302	0.8543

35hi 2008			Prediction Probability Matrix							
Class	Ave Depth (cm)	Total Area (ha)	Carex	Senescent	Equisetum	Phragmites	Scirpus	Trees	Typha	Water
Carex	11.6348	20.7715	0.6732	0.0011	0.0991	0.1405	0.0029	0.0150	0.0500	0.0181
Senescent	30.5069	50.0150	0.0030	0.9702	0.0007	0.0069	0.0058	0.0000	0.0124	0.0010
Equisetum	16.1633	6.3654	0.1583	0.0000	0.6368	0.0957	0.0012	0.0836	0.0110	0.0132
Phragmites	34.6900	55.1963	0.0986	0.0028	0.0414	0.6533	0.0384	0.0077	0.1331	0.0246
Scirpus	50.0874	8.8617	0.0216	0.0048	0.0068	0.0980	0.6679	0.0001	0.1387	0.0623
Trees	11.4827	29.7183	0.0148	0.0001	0.0276	0.0103	0.0002	0.9436	0.0016	0.0019
Typha	42.3129	8.2158	0.0832	0.0329	0.0257	0.1369	0.1412	0.0007	0.5633	0.0160
Water	58.5592	29.6869	0.0231	0.0010	0.0075	0.0404	0.0470	0.0012	0.0224	0.8572

35hi 2009			Prediction Probability Matrix							
Class	Ave Depth (cm)	Total Area (ha)	Carex	Senescent	Equisetum	Phragmites	Scirpus	Trees	Typha	Water
Carex	18.4230	15.3638	0.6494	0.0111	0.0501	0.1873	0.0051	0.0136	0.0734	0.0099
Senescent	30.6831	64.0441	0.0030	0.9893	0.0003	0.0043	0.0010	0.0000	0.0014	0.0005
Equisetum	27.5808	2.9904	0.1535	0.0000	0.5297	0.1513	0.0539	0.0292	0.0526	0.0297
Phragmites	37.3594	41.2388	0.0991	0.0032	0.0412	0.6544	0.0823	0.0014	0.1025	0.0158
Scirpus	52.5728	7.2014	0.0210	0.0052	0.0234	0.1733	0.6529	0.0004	0.0730	0.0507
Trees	11.3522	41.1835	0.0096	0.0005	0.0052	0.0048	0.0010	0.9771	0.0011	0.0006
Typha	49.8870	3.4622	0.1156	0.0018	0.0451	0.2044	0.0981	0.0000	0.4896	0.0453
Water	56.0000	33.3856	0.0252	0.0007	0.0095	0.0356	0.0304	0.0007	0.0190	0.8787

Fig. 6. Quickbird® imagery, vegetation classification, confusion matrices, species class changes over time in wetland 35hi, a partial drawdown wetland, 2007-2009 at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

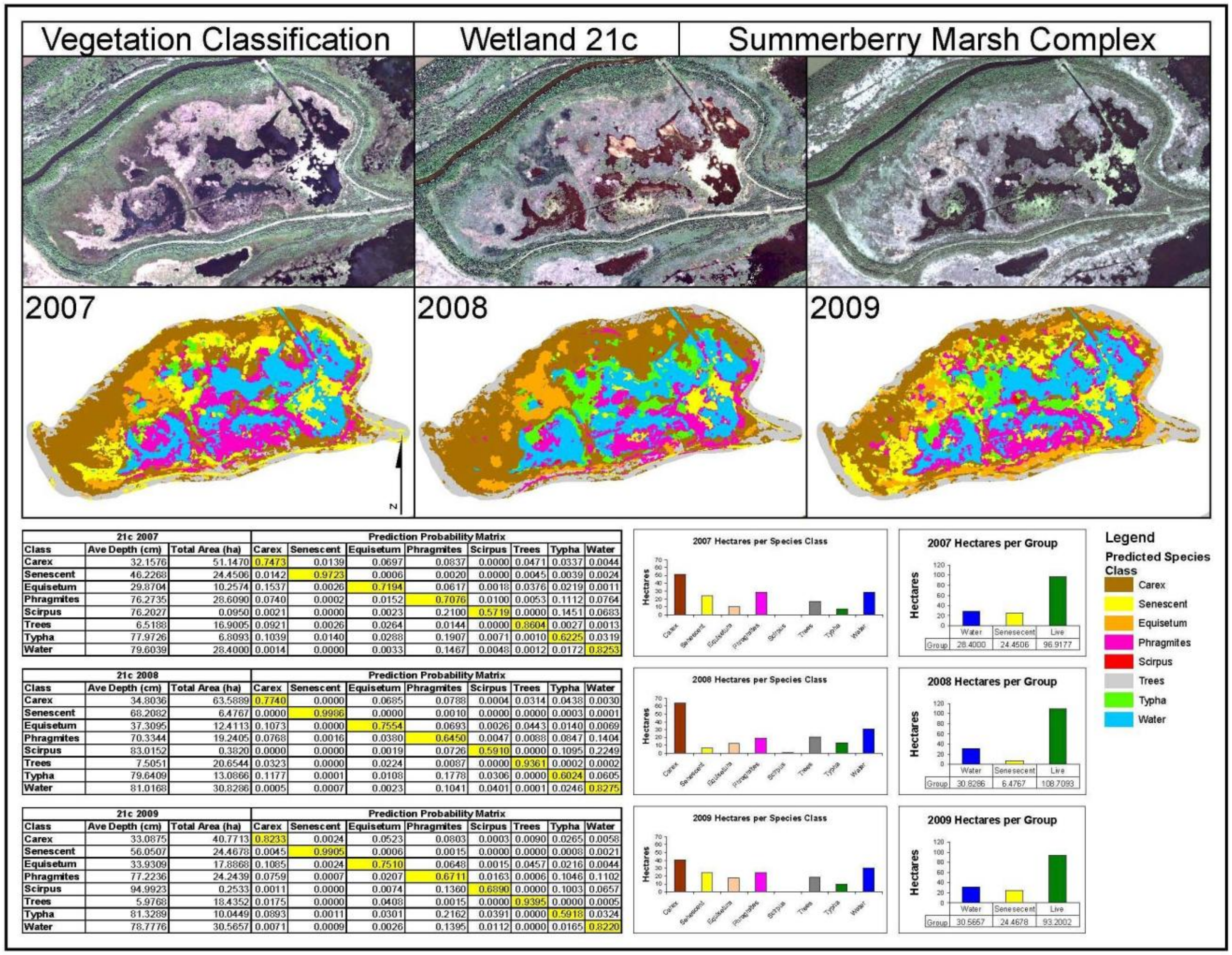


37c 2007			Prediction Probability Matrix							
Class	Ave Depth (cm)	Total Area (ha)	Carex	Senescent	Equisetum	Phragmites	Scirpus	Trees	Typha	Water
Carex	44.9247	103.2761	0.7797	0.0022	0.0144	0.1192	0.0015	0.0120	0.0683	0.0027
Senescent	98.5444	11.2593	0.0125	0.9242	0.0012	0.0168	0.0141	0.0029	0.0276	0.0006
Equisetum	49.7542	0.2842	0.1565	0.0007	0.6649	0.0576	0.0034	0.0025	0.1083	0.0061
Phragmites	85.2573	15.2038	0.1914	0.0079	0.0159	0.5613	0.0170	0.0060	0.1933	0.0071
Scirpus	113.6837	20.0326	0.0025	0.0092	0.0050	0.0207	0.8541	0.0000	0.0885	0.0199
Trees	13.4050	18.4809	0.0447	0.0043	0.0023	0.0180	0.0000	0.9255	0.0052	0.0000
Typha	91.1640	30.0791	0.1010	0.0117	0.0155	0.1792	0.0381	0.0016	0.6498	0.0030
Water	110.7375	30.2742	0.0496	0.0010	0.0022	0.0255	0.0846	0.0001	0.0343	0.8026

37c 2008			Prediction Probability Matrix							
Class	Ave Depth (cm)	Total Area (ha)	Carex	Senescent	Equisetum	Phragmites	Scirpus	Trees	Typha	Water
Carex	7.0529	61.2357	0.7777	0.0028	0.0415	0.1168	0.0055	0.0049	0.0320	0.0187
Senescent	26.1338	72.9591	0.0049	0.9737	0.0013	0.0037	0.0072	0.0000	0.0091	0.0000
Equisetum	5.9002	2.7263	0.1357	0.0000	0.6093	0.1731	0.0041	0.0503	0.0067	0.0204
Phragmites	25.2720	17.9420	0.1763	0.0015	0.0753	0.5508	0.0344	0.0116	0.1359	0.0142
Scirpus	52.1031	23.8236	0.0145	0.0058	0.0035	0.0312	0.7768	0.0004	0.1097	0.0579
Trees	2.5719	8.7164	0.0079	0.0000	0.0159	0.0096	0.0000	0.9643	0.0022	0.0000
Typha	38.0925	11.8264	0.0902	0.0181	0.0355	0.1239	0.1231	0.0000	0.5770	0.0322
Water	48.4344	29.4181	0.0784	0.0000	0.0067	0.0148	0.0683	0.0000	0.0247	0.8070

37c 2009			Prediction Probability Matrix							
Class	Ave Depth (cm)	Total Area (ha)	Carex	Senescent	Equisetum	Phragmites	Scirpus	Trees	Typha	Water
Carex	12.1771	12.7084	0.6970	0.0168	0.0519	0.1083	0.0071	0.0273	0.0792	0.0123
Senescent	20.7887	119.0415	0.0031	0.9922	0.0001	0.0018	0.0013	0.0002	0.0011	0.0001
Equisetum	27.3881	1.5511	0.1306	0.0000	0.5530	0.1179	0.0718	0.0157	0.0749	0.0361
Phragmites	30.5948	17.8425	0.1036	0.0081	0.0331	0.6127	0.1064	0.0002	0.1125	0.0233
Scirpus	50.8108	28.5875	0.0131	0.0033	0.0211	0.0857	0.7985	0.0016	0.0349	0.0417
Trees	2.8402	21.3264	0.0178	0.0000	0.0028	0.0025	0.0002	0.9741	0.0015	0.0011
Typha	39.7687	2.2446	0.1539	0.0052	0.0390	0.1965	0.0951	0.0079	0.4860	0.0163
Water	45.5961	25.3363	0.0367	0.0000	0.0120	0.0232	0.0662	0.0045	0.0157	0.8417

Fig. 7. Quickbird® imagery, vegetation classification, confusion matrices, species class changes over time in wetland 37c, a partial drawdown wetland, 2007-2009 at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

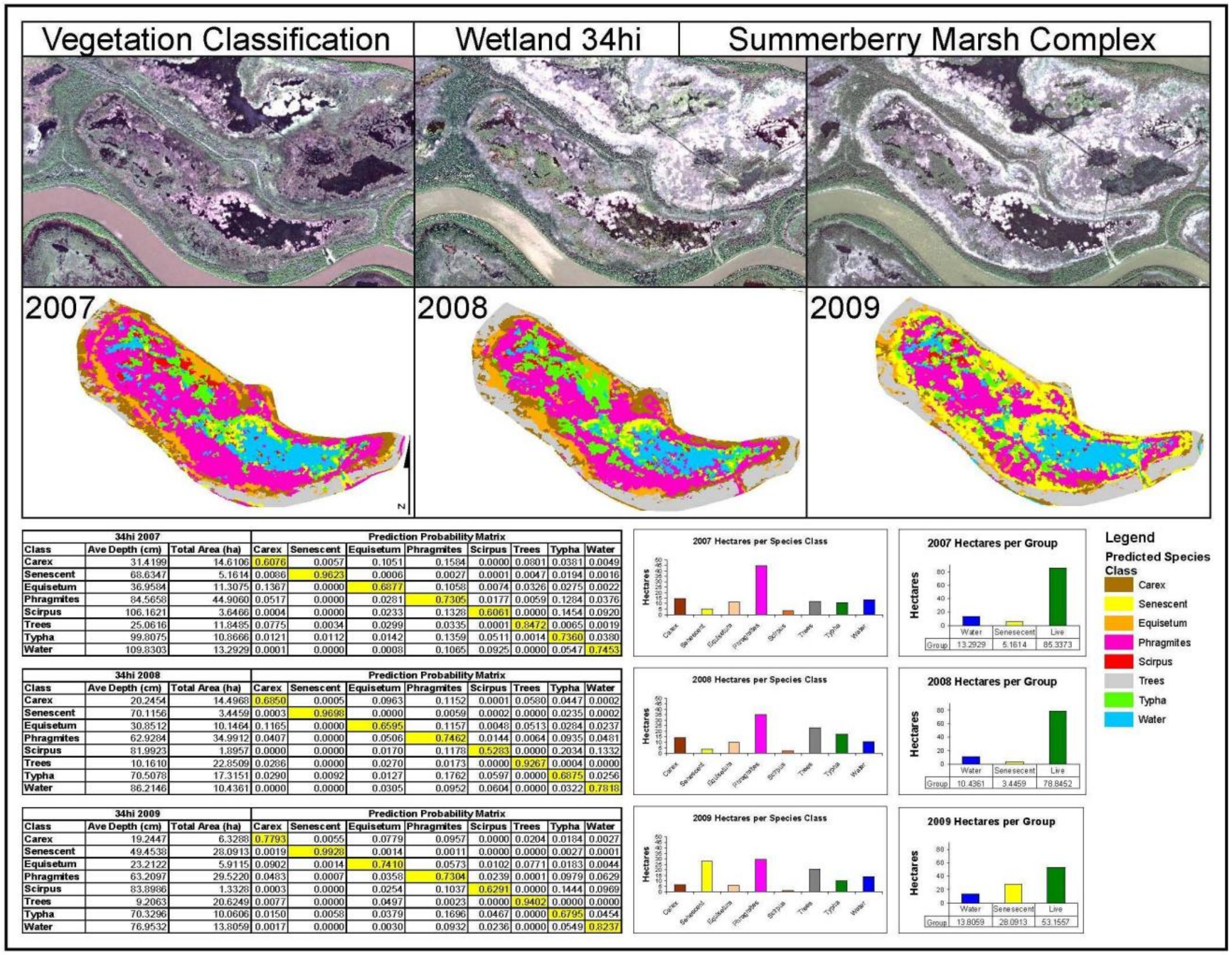


21c 2007			Prediction Probability Matrix							
Class	Ave Depth (cm)	Total Area (ha)	Carex	Senescent	Equisetum	Phragmites	Scirpus	Trees	Typha	Water
Carex	32.1576	51.1470	0.7473	0.0139	0.0697	0.0837	0.0000	0.0471	0.0337	0.0044
Senescent	46.2268	24.4506	0.0142	0.9723	0.0006	0.0020	0.0000	0.0045	0.0039	0.0024
Equisetum	29.8704	10.2574	0.1537	0.0026	0.7194	0.0617	0.0018	0.0376	0.0219	0.0011
Phragmites	76.2735	28.6090	0.0740	0.0002	0.0152	0.7076	0.0100	0.0053	0.1112	0.0764
Scirpus	76.2027	0.0950	0.0021	0.0000	0.0023	0.2100	0.5719	0.0000	0.1451	0.0683
Trees	6.5188	16.9005	0.0921	0.0026	0.0264	0.0144	0.0000	0.8604	0.0027	0.0013
Typha	77.9726	6.8093	0.1039	0.0140	0.0288	0.1907	0.0071	0.0010	0.6225	0.0319
Water	79.6039	28.4000	0.0014	0.0000	0.0033	0.1467	0.0048	0.0012	0.0172	0.8253

21c 2008			Prediction Probability Matrix							
Class	Ave Depth (cm)	Total Area (ha)	Carex	Senescent	Equisetum	Phragmites	Scirpus	Trees	Typha	Water
Carex	34.8036	63.5889	0.7740	0.0000	0.0685	0.0788	0.0004	0.0314	0.0438	0.0030
Senescent	68.2082	6.4767	0.0000	0.9986	0.0000	0.0010	0.0000	0.0000	0.0003	0.0001
Equisetum	37.3095	12.4113	0.1073	0.0000	0.7554	0.0693	0.0026	0.0443	0.0140	0.0069
Phragmites	70.3344	19.2405	0.0768	0.0016	0.0380	0.6450	0.0047	0.0088	0.0847	0.1404
Scirpus	83.0152	0.3820	0.0000	0.0000	0.0019	0.0726	0.5910	0.0000	0.1095	0.2249
Trees	7.5051	20.6544	0.0323	0.0000	0.0224	0.0087	0.0000	0.9361	0.0002	0.0002
Typha	79.6409	13.0866	0.1177	0.0001	0.0108	0.1778	0.0306	0.0000	0.6024	0.0605
Water	81.0168	30.8286	0.0005	0.0007	0.0023	0.1041	0.0401	0.0001	0.0246	0.8275

21c 2009			Prediction Probability Matrix							
Class	Ave Depth (cm)	Total Area (ha)	Carex	Senescent	Equisetum	Phragmites	Scirpus	Trees	Typha	Water
Carex	33.0875	40.7713	0.8233	0.0024	0.0523	0.0803	0.0003	0.0090	0.0265	0.0058
Senescent	56.0507	24.4678	0.0045	0.9905	0.0006	0.0015	0.0000	0.0000	0.0008	0.0021
Equisetum	33.9309	17.8868	0.1085	0.0024	0.7510	0.0648	0.0015	0.0457	0.0216	0.0044
Phragmites	77.2236	24.2439	0.0759	0.0007	0.0207	0.6711	0.0163	0.0006	0.1046	0.1102
Scirpus	94.9923	0.2533	0.0011	0.0000	0.0074	0.1360	0.6890	0.0000	0.1003	0.0657
Trees	5.9768	18.4352	0.0175	0.0000	0.0408	0.0015	0.0000	0.9395	0.0000	0.0005
Typha	81.3289	10.0449	0.0893	0.0011	0.0301	0.2162	0.0391	0.0000	0.5918	0.0324
Water	78.7776	30.5657	0.0071	0.0009	0.0026	0.1395	0.0112	0.0000	0.0165	0.8220

Fig. 8. Quickbird® imagery, vegetation classification, confusion matrices, species class changes over time in wetland 21c, a full supply level wetland, 2007-2009 at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.



34hi 2007			Prediction Probability Matrix							
Class	Ave Depth (cm)	Total Area (ha)	Carex	Senescent	Equisetum	Phragmites	Scirpus	Trees	Typha	Water
Carex	31.4199	14.6106	0.6076	0.0057	0.1051	0.1584	0.0000	0.0801	0.0381	0.0049
Senescent	68.6347	5.1614	0.0086	0.9623	0.0006	0.0027	0.0001	0.0047	0.0194	0.0016
Equisetum	36.9584	11.3075	0.1367	0.0000	0.6877	0.1058	0.0074	0.0326	0.0275	0.0022
Phragmites	84.5658	44.9060	0.0517	0.0000	0.0281	0.7305	0.0177	0.0059	0.1284	0.0376
Scirpus	106.1621	3.6466	0.0004	0.0000	0.0233	0.1328	0.6061	0.0000	0.1454	0.0920
Trees	25.0616	11.8485	0.0775	0.0034	0.0299	0.0335	0.0001	0.8472	0.0065	0.0019
Typha	99.8075	10.8666	0.0121	0.0112	0.0142	0.1359	0.0511	0.0014	0.7360	0.0380
Water	109.8303	13.2929	0.0001	0.0000	0.0008	0.1065	0.0925	0.0000	0.0547	0.7453

34hi 2008			Prediction Probability Matrix							
Class	Ave Depth (cm)	Total Area (ha)	Carex	Senescent	Equisetum	Phragmites	Scirpus	Trees	Typha	Water
Carex	20.2454	14.4968	0.6850	0.0005	0.0963	0.1152	0.0001	0.0580	0.0447	0.0002
Senescent	70.1156	3.4459	0.0003	0.9698	0.0000	0.0059	0.0002	0.0000	0.0235	0.0002
Equisetum	30.8512	10.1464	0.1165	0.0000	0.6595	0.1157	0.0048	0.0513	0.0284	0.0237
Phragmites	62.9284	34.9912	0.0407	0.0000	0.0506	0.7462	0.0144	0.0064	0.0935	0.0481
Scirpus	81.9923	1.8957	0.0000	0.0000	0.0170	0.1178	0.5283	0.0000	0.2034	0.1332
Trees	10.1610	22.8509	0.0286	0.0000	0.0270	0.0173	0.0000	0.9267	0.0004	0.0000
Typha	70.5078	17.3151	0.0290	0.0092	0.0127	0.1762	0.0597	0.0000	0.6875	0.0256
Water	86.2146	10.4361	0.0000	0.0000	0.0305	0.0952	0.0604	0.0000	0.0322	0.7818

34hi 2009			Prediction Probability Matrix							
Class	Ave Depth (cm)	Total Area (ha)	Carex	Senescent	Equisetum	Phragmites	Scirpus	Trees	Typha	Water
Carex	19.2447	6.3288	0.7793	0.0055	0.0779	0.0957	0.0000	0.0204	0.0184	0.0027
Senescent	49.4538	28.0913	0.0019	0.9928	0.0014	0.0011	0.0000	0.0000	0.0027	0.0001
Equisetum	23.2122	5.9115	0.0902	0.0014	0.7410	0.0573	0.0102	0.0771	0.0183	0.0044
Phragmites	63.2097	29.5220	0.0483	0.0007	0.0358	0.7304	0.0239	0.0001	0.0979	0.0629
Scirpus	83.8986	1.3328	0.0003	0.0000	0.0254	0.1037	0.6291	0.0000	0.1444	0.0969
Trees	9.2063	20.6249	0.0077	0.0000	0.0497	0.0023	0.0000	0.9402	0.0000	0.0000
Typha	70.3296	10.0606	0.0150	0.0058	0.0379	0.1696	0.0467	0.0000	0.6795	0.0454
Water	76.9532	13.8059	0.0017	0.0000	0.0030	0.0932	0.0236	0.0000	0.0549	0.8237

Fig. 9. Quickbird® imagery, vegetation classification, confusion matrices, species class changes over time in wetland 34hi, a full supply level wetland, 2007-2009 at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

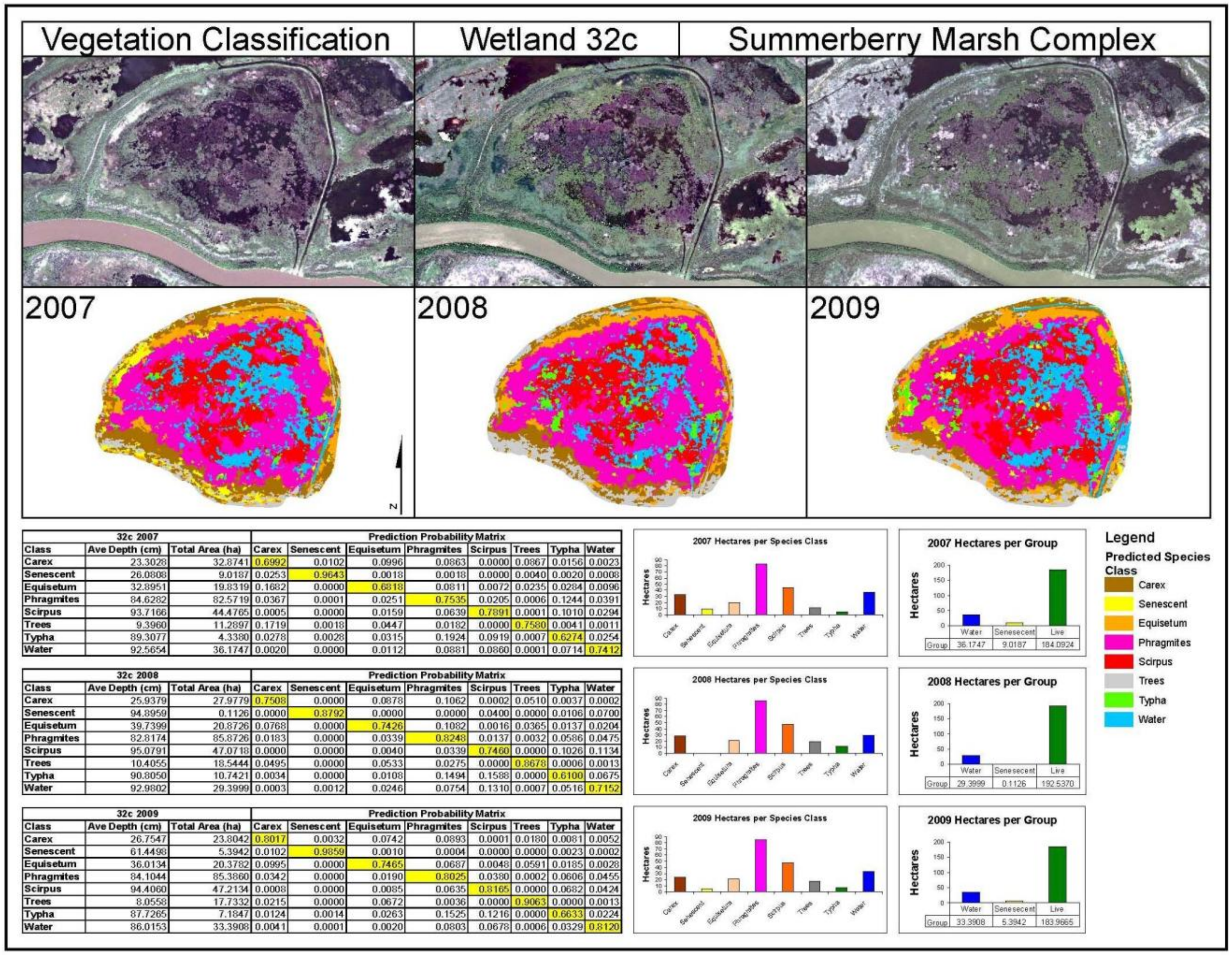


Fig. 10. Quickbird® imagery, vegetation classification, confusion matrices, species class changes over time in wetland 32c, a full supply level wetland, 2007-2009 at the Summerberry Marsh Complex, The Pas, Manitoba, Canada.

APPENDIX C: HISTORICAL MUSKRAT HOUSE COUNTS

Table 1: Surface area (ha), calcualted from water levels at the time of study, of wetland basins surveyed for muskrat (*Ondatra zibethicus*) houses in the Saskatchewan River Delta from 1980-1989.

Basin	1980 Area (ha)	1981 Area (ha)	1982 Area (ha)	1983 Area (ha)	1984 Area (ha)	1985 Area (ha)	1986 Area (ha)	1987 Area (ha)	1988 Area (ha)	1989 Area (ha)
Ravensnest	719	* 339	† 0	‡ 735	445	792	623	858	761	810
5-6R	42	43	43	42	39	38	57	57	40	53
8-9R	† 0	‡ 679	808	679	712	1026	922	1079	1028	1029
12-13-14R	91	95	94	† 60	§ 101	117	109	115	121	122
15R	11	16	14	35	14	17	† 0	§ 12	‡ 22	24
23-24-25NBC	n/a	75	87	101	85	* 38	§ 59	‡ 105	121	101
20-31-33C	525	394	384	440	425	428	514	518	399	517
21C	113	121	† 4	‡ 88	102	116	90	113	127	133
22-26-27C	408	398	440	457	425	432	437	437	* 363	* 587
32C	n/a	195	194	198	* 0	‡ 195	200	206	196	198
34-37C	452	549	469	537	384	537	445	425	397	429
38-40C	49	57	86	78	66	86	163	113	146	174
33-35HI	35	56	33	47	39	33	54	63	49	57

* - indicates basin in partial drawdown (> 25% of basin area is shallowly flooded)
† - indicates basin in complete drawdown (< 25% of basin area is shallowly flooded)
‡ - indicates basin refilled to operating level
§ - indicates basin partially refilled (> 0.5 ft below operating level)

Table 1: Continued

Basin	1980 Area (ha)	1981 Area (ha)	1982 Area (ha)	1983 Area (ha)	1984 Area (ha)	1985 Area (ha)	1986 Area (ha)	1987 Area (ha)	1988 Area (ha)	1989 Area (ha)
34HI	n/a	80	80	78	74	80	81	* 61	* 53	‡ 83
36HI	n/a	74	82	79	† 0	§ 51	58	70	61	81
39HI	n/a	49	44	* 21	‡ 38	44	47	48	42	45
28UHI	n/a	90	87	87	86	* 30	§ 59	‡ 84	91	86
8K	n/a	183	178	204	192	181	196	* 77	§ 130	‡ 200
26K	n/a	* 93	* 67	‡ 360	368	396	392	406	393	389
36K	566	* 566	* 622	‡ 719	676	711	736	842	688	851
51 52 UKI	n/a	72	68	70	59	19	62	59	45	* 59
Saskeram	7595	7838	6706	7110	7204	7272	7446	7827	7366	7695
Birch Lake	3474	2990	2384	2828	3521	3152	* 1659	* 1538	§ 1416	‡ 2471
Lake 6	1667	1636	1384	1605	2044	1626	1598	1457	1113	1782
Elm Creek	1434	1434	1656	2141	1983	2101	2185	2133	1983	2066
Reader	7353	7353	6908	7595	8074	7595	7902	7649	6799	6764

* - indicates basin in partial drawdown (> 25% of basin area is shallowly flooded)
† - indicates basin in complete drawdown (< 25% of basin area is shallowly flooded)
‡ - indicates basin refilled to operating level
§ - indicates basin partially refilled (> 0.5 ft below operating level)

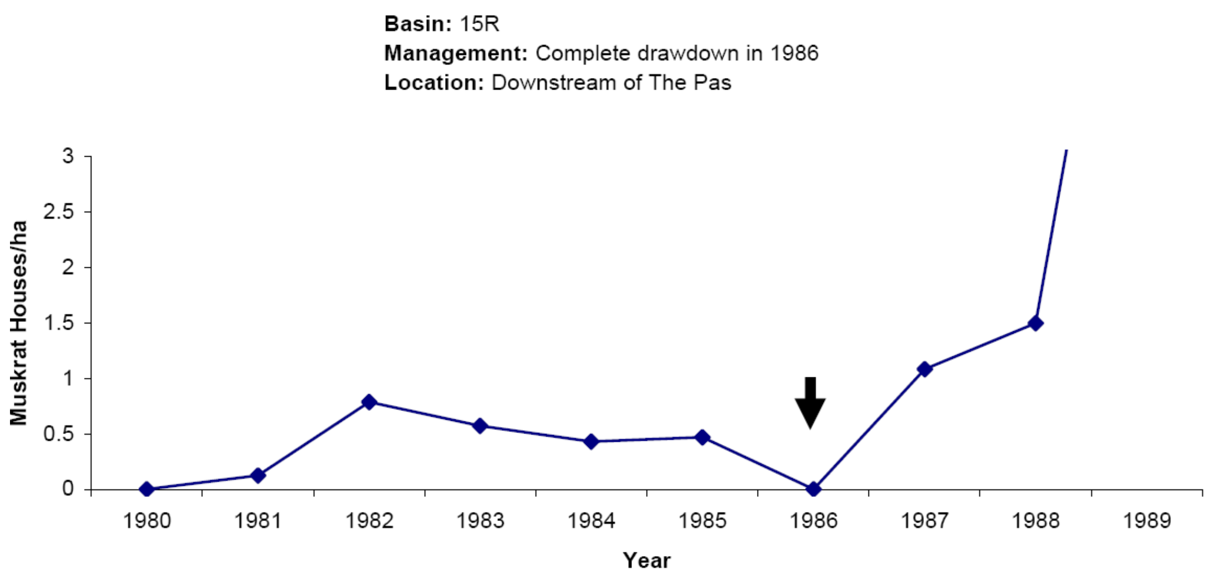


Fig. 1. Muskrat (*Ondatra zibethicus*) house counts of wetlands 15R from 1980-1989 in the Saskatchewan River Delta.

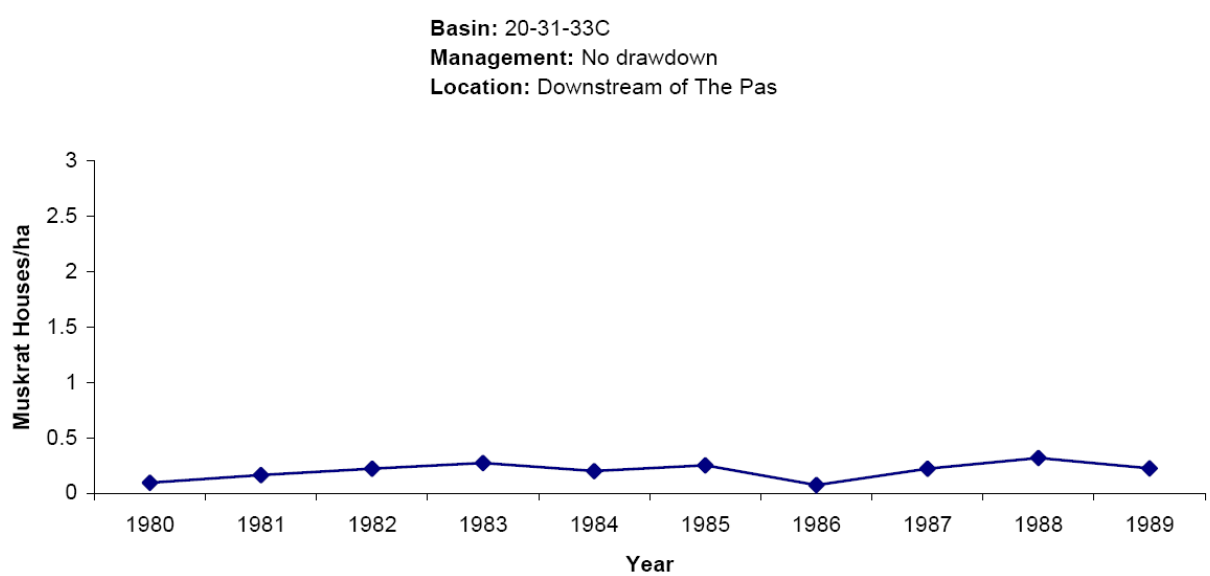


Fig. 2. Muskrat (*Ondatra zibethicus*) house counts of wetlands 20-31-33C from 1980-1989 in the Saskatchewan River Delta.

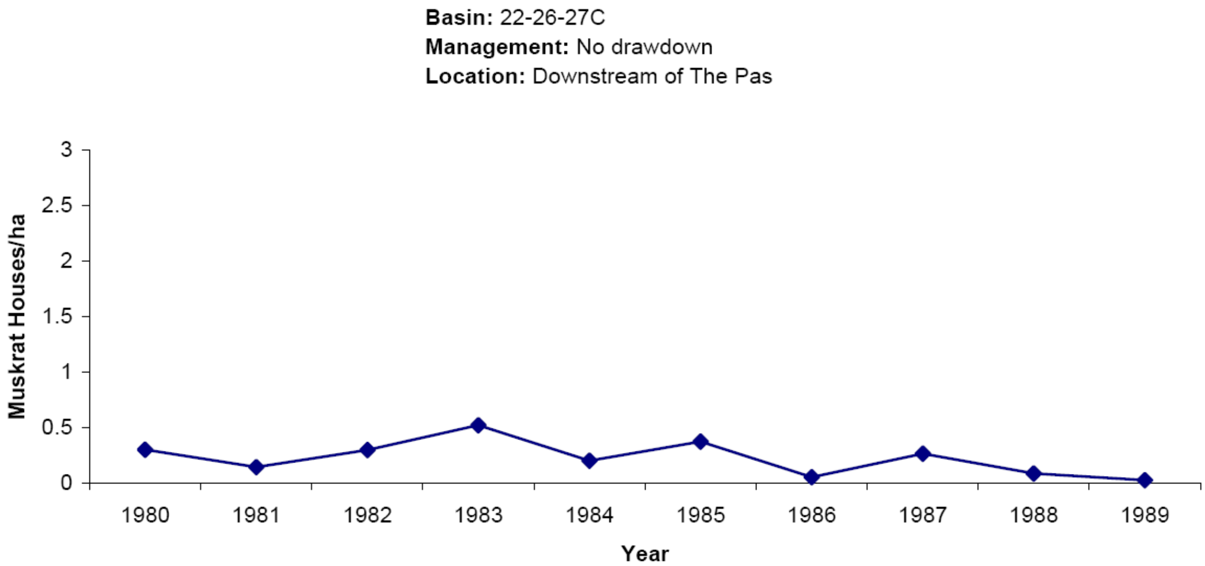


Fig. 3. Muskrat (*Ondatra zibethicus*) house counts of wetlands 22-26-27C from 1980-1989 in the Saskatchewan River Delta.

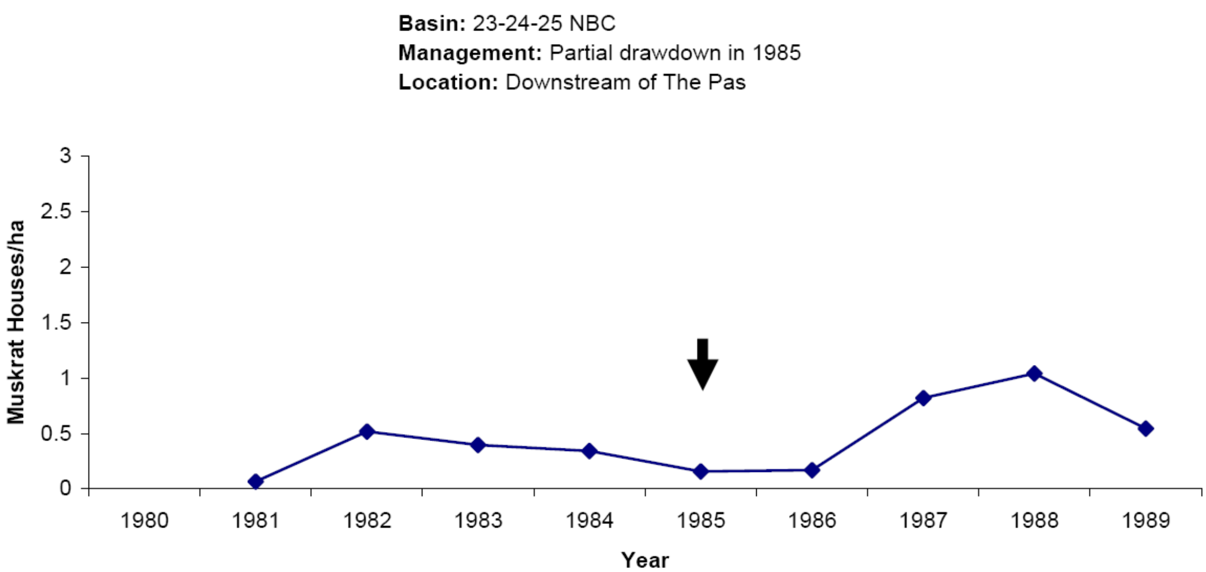


Fig. 4. Muskrat (*Ondatra zibethicus*) house counts of wetlands 23-24-25NBC from 1980-1989 in the Saskatchewan River Delta.

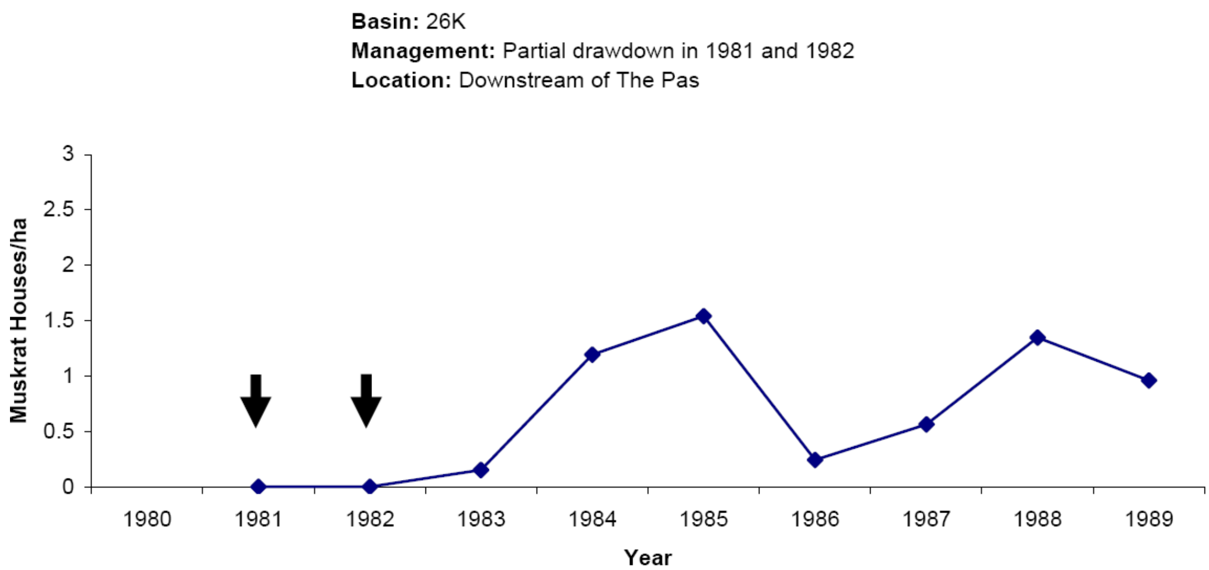


Fig. 5. Muskrat (*Ondatra zibethicus*) house counts of wetlands 26K from 1980-1989 in the Saskatchewan River Delta.

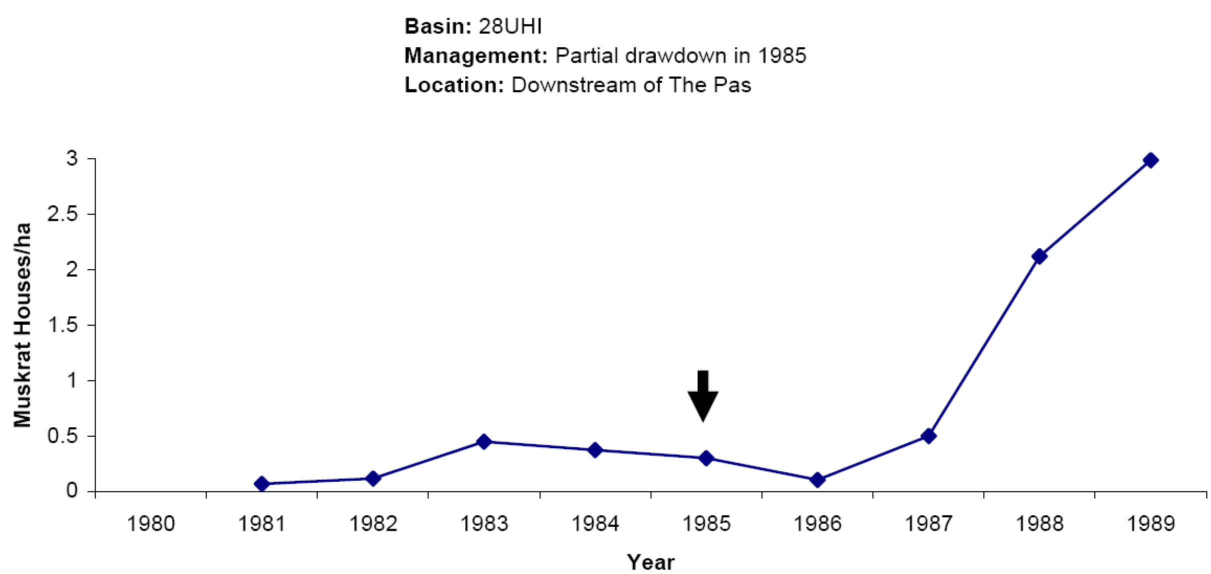


Fig. 6. Muskrat (*Ondatra zibethicus*) house counts of wetlands 28UHI from 1980-1989 in the Saskatchewan River Delta.

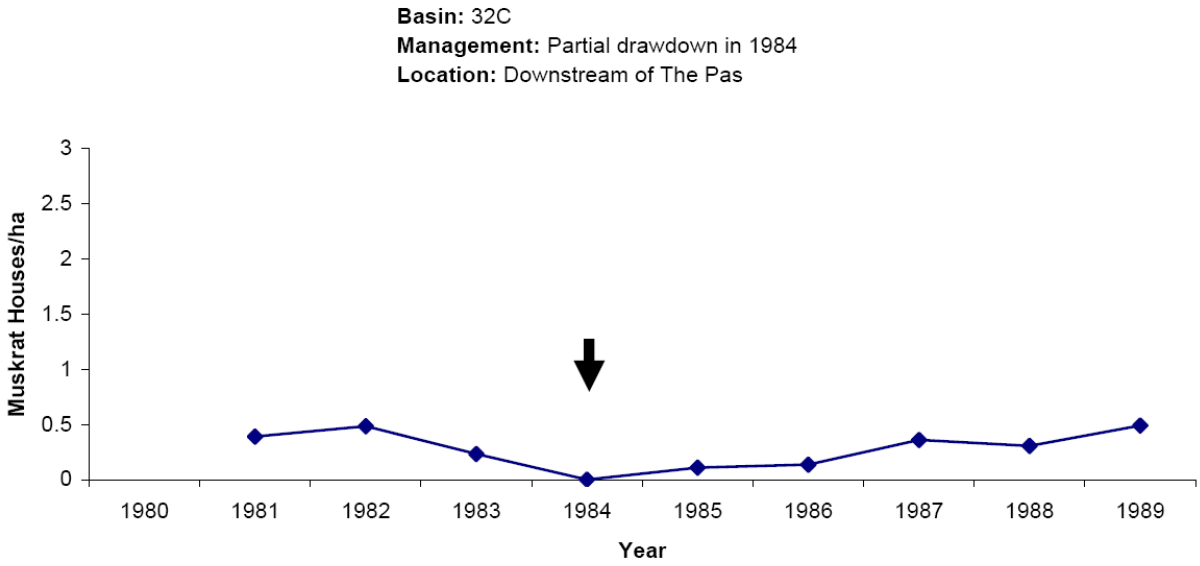


Fig. 7. Muskrat (*Ondatra zibethicus*) house counts of wetlands 32C from 1980-1989 in the Saskatchewan River Delta.

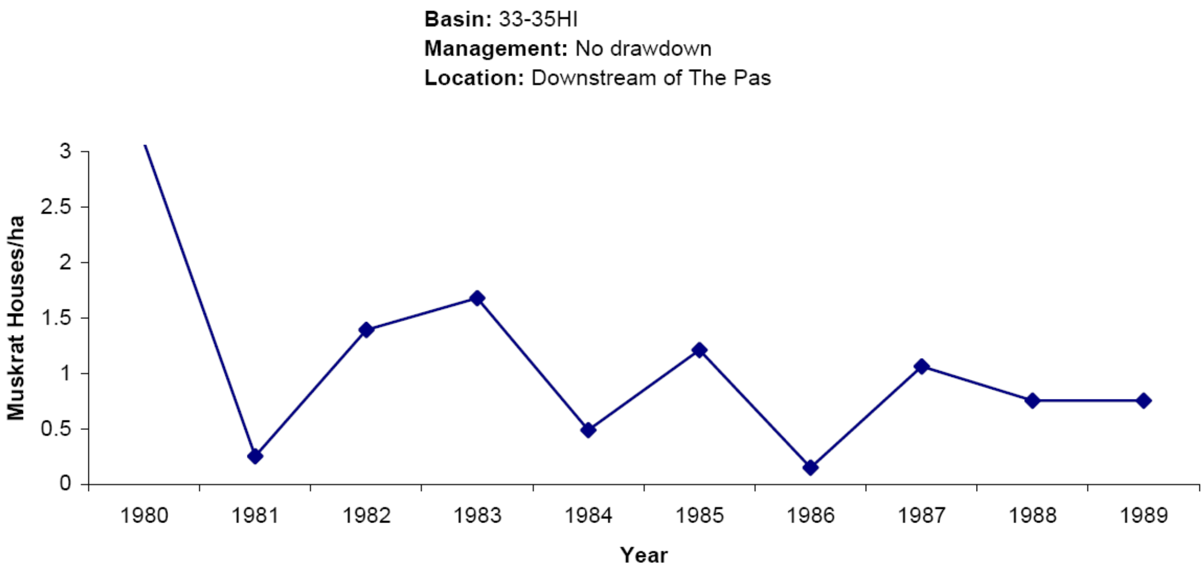


Fig. 8. Muskrat (*Ondatra zibethicus*) house counts of wetlands 33-35HI from 1980-1989 in the Saskatchewan River Delta.

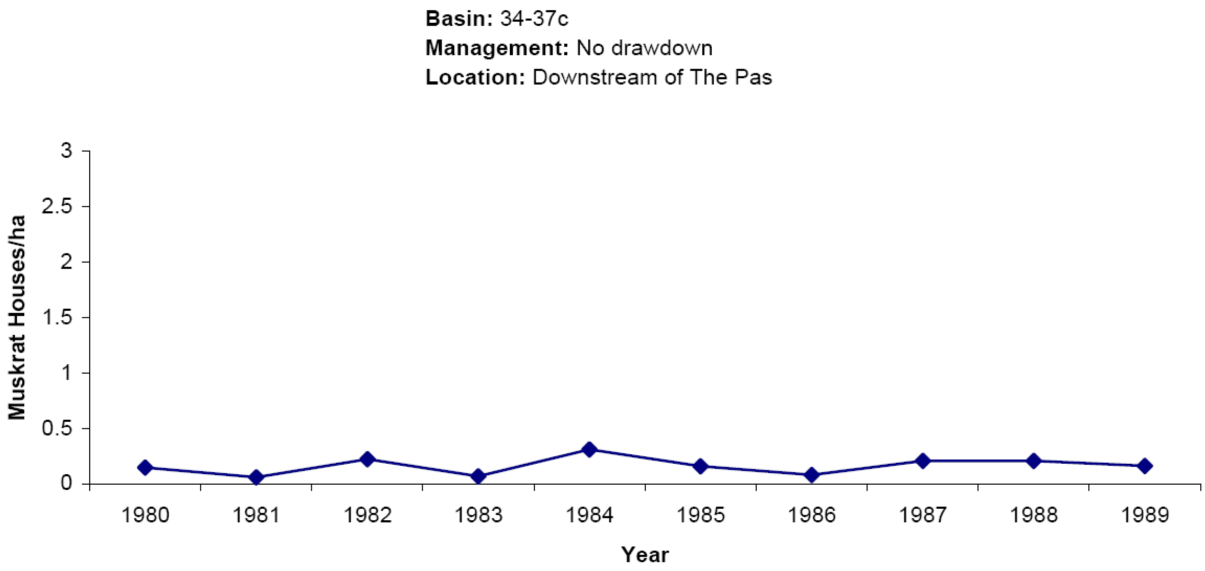


Fig. 9. Muskrat (*Ondatra zibethicus*) house counts of wetlands 34-37C from 1980-1989 in the Saskatchewan River Delta.

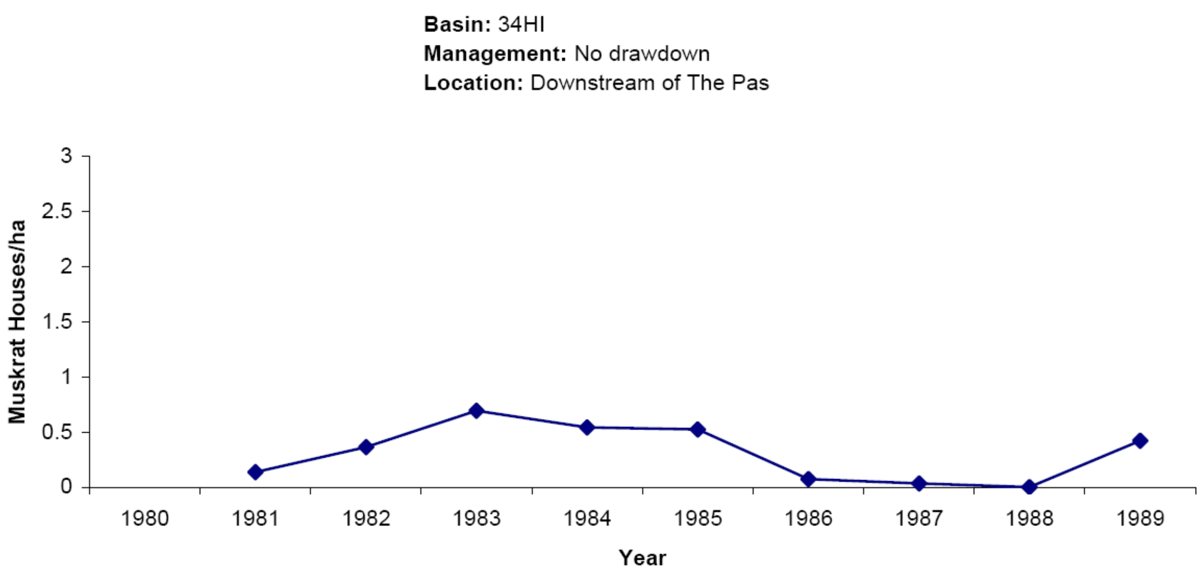


Fig. 10. Muskrat (*Ondatra zibethicus*) house counts of wetlands 34HI from 1980-1989 in the Saskatchewan River Delta.

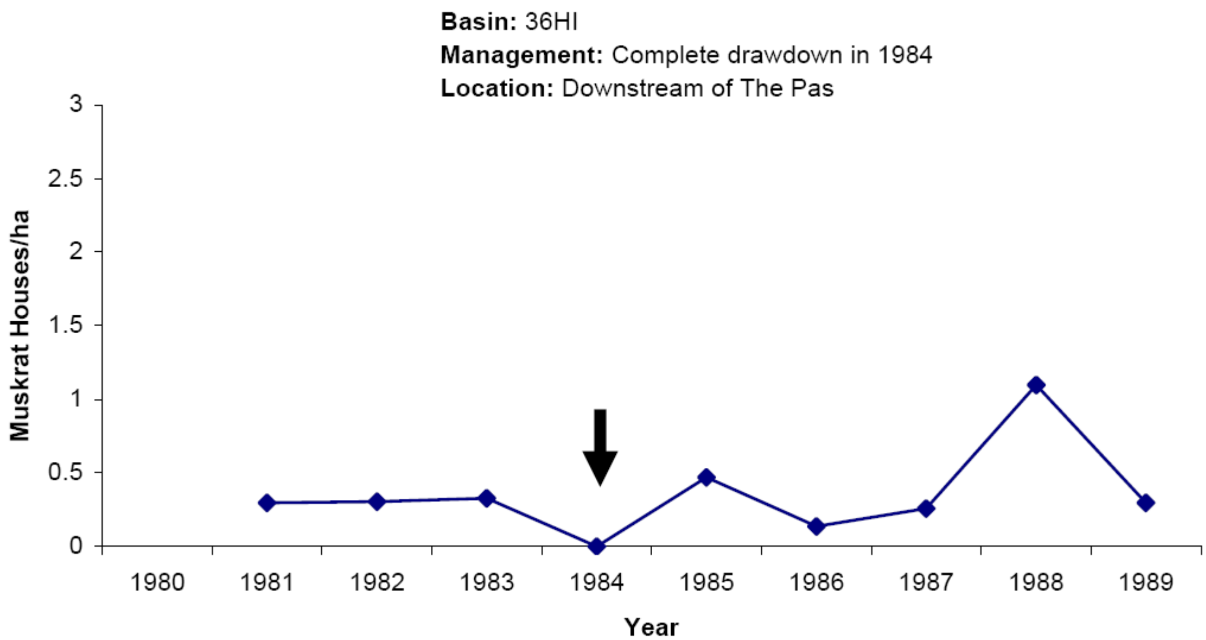


Fig. 11. Muskrat (*Ondatra zibethicus*) house counts of wetlands 36HI from 1980-1989 in the Saskatchewan River Delta.

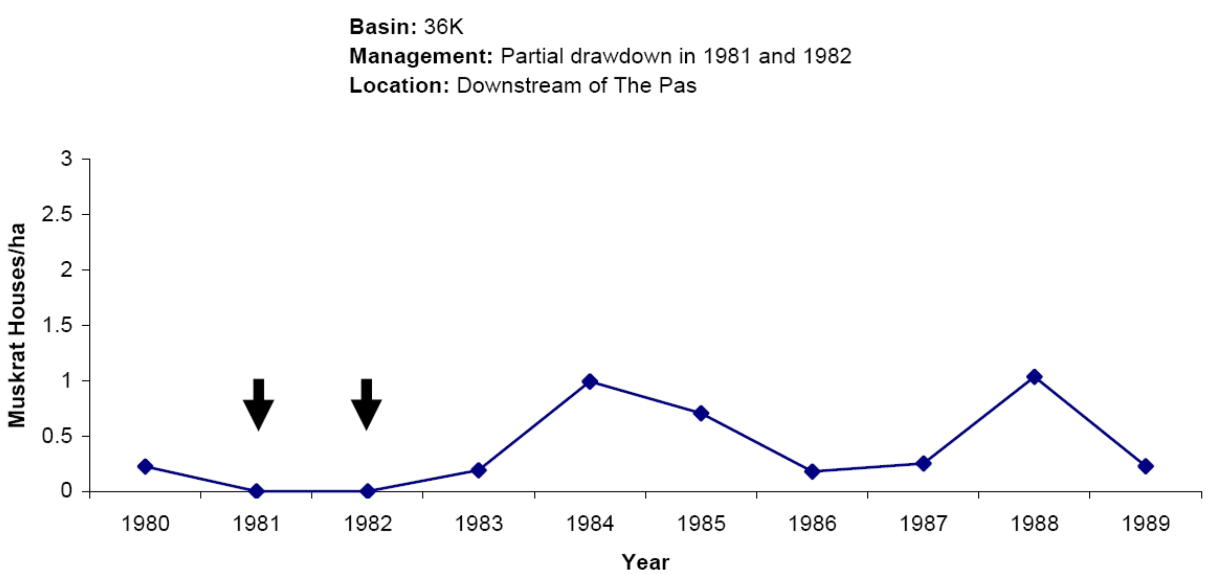


Fig. 12. Muskrat (*Ondatra zibethicus*) house counts of wetlands 36K from 1980-1989 in the Saskatchewan River Delta.

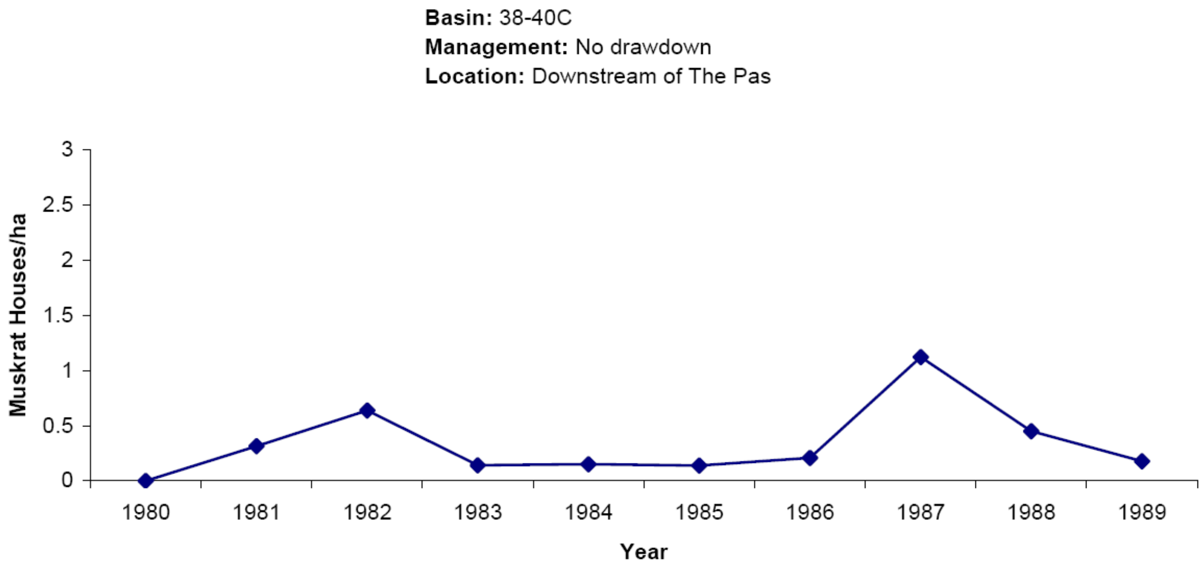


Fig. 13. Muskrat (*Ondatra zibethicus*) house counts of wetlands 38-40C from 1980-1989 in the Saskatchewan River Delta.

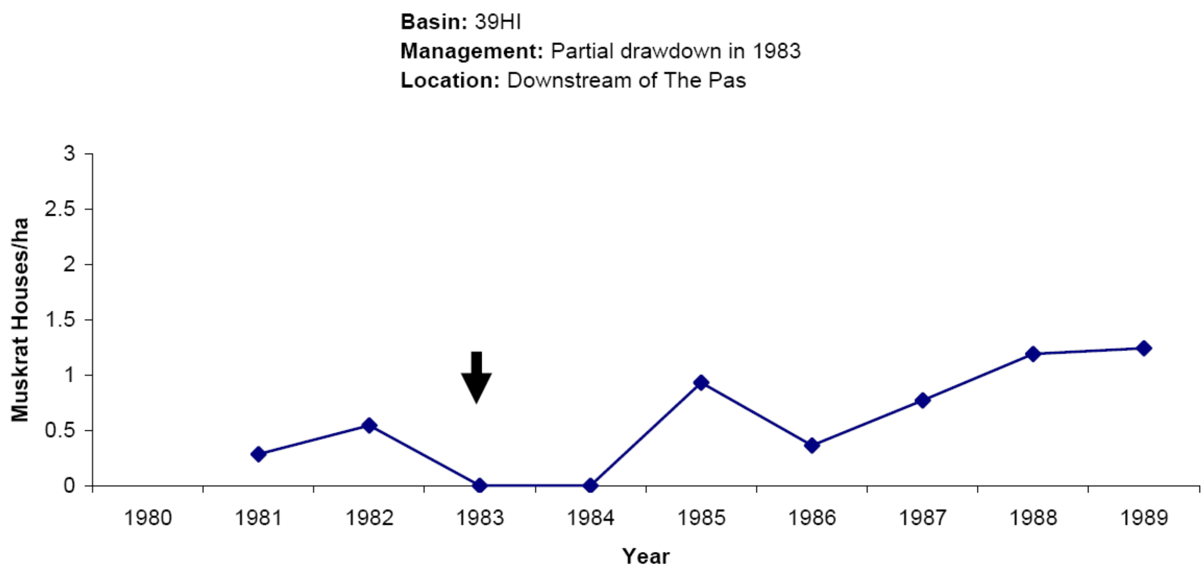


Fig. 14. Muskrat (*Ondatra zibethicus*) house counts of wetlands 39HI from 1980-1989 in the Saskatchewan River Delta.

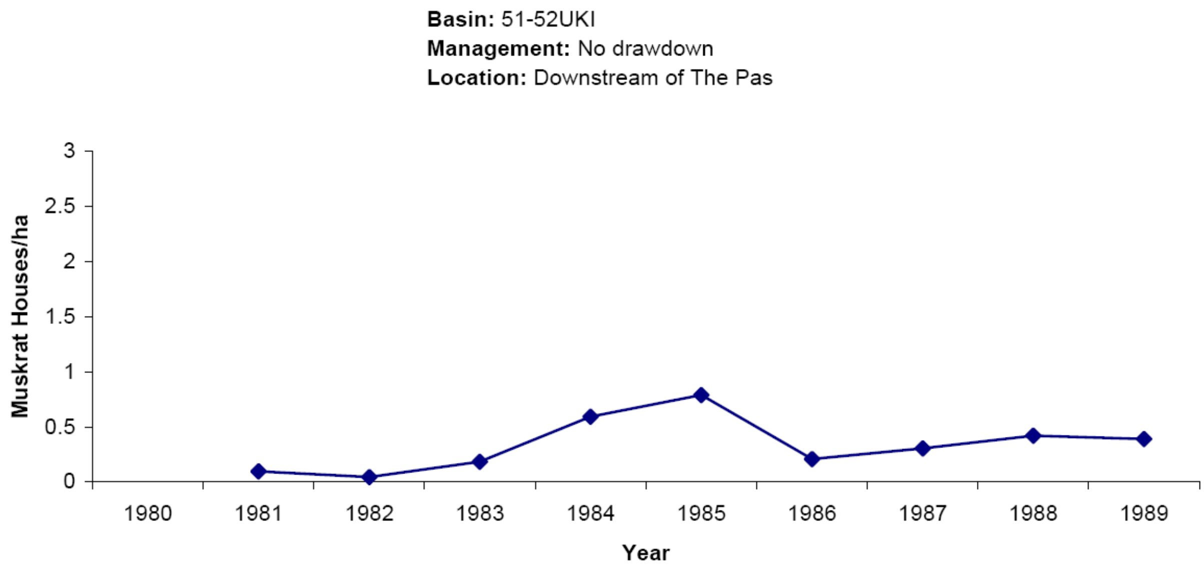


Fig. 15. Muskrat (*Ondatra zibethicus*) house counts of wetlands 51-52UKI from 1980-1989 in the Saskatchewan River Delta.

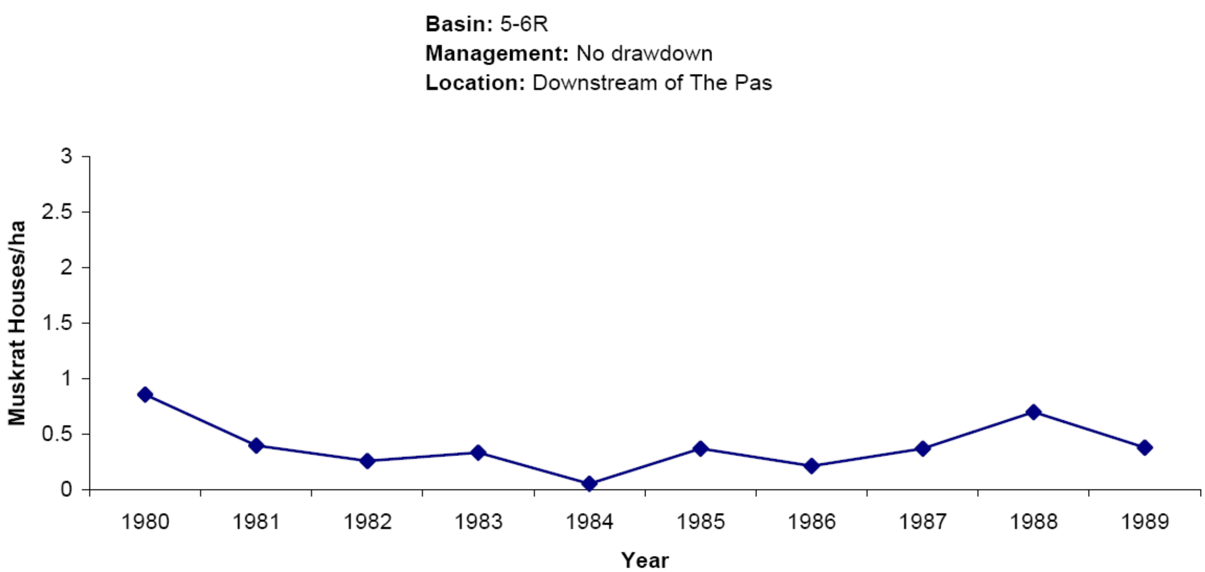


Fig. 16. Muskrat (*Ondatra zibethicus*) house counts of wetlands 5-6R from 1980-1989 in the Saskatchewan River Delta.

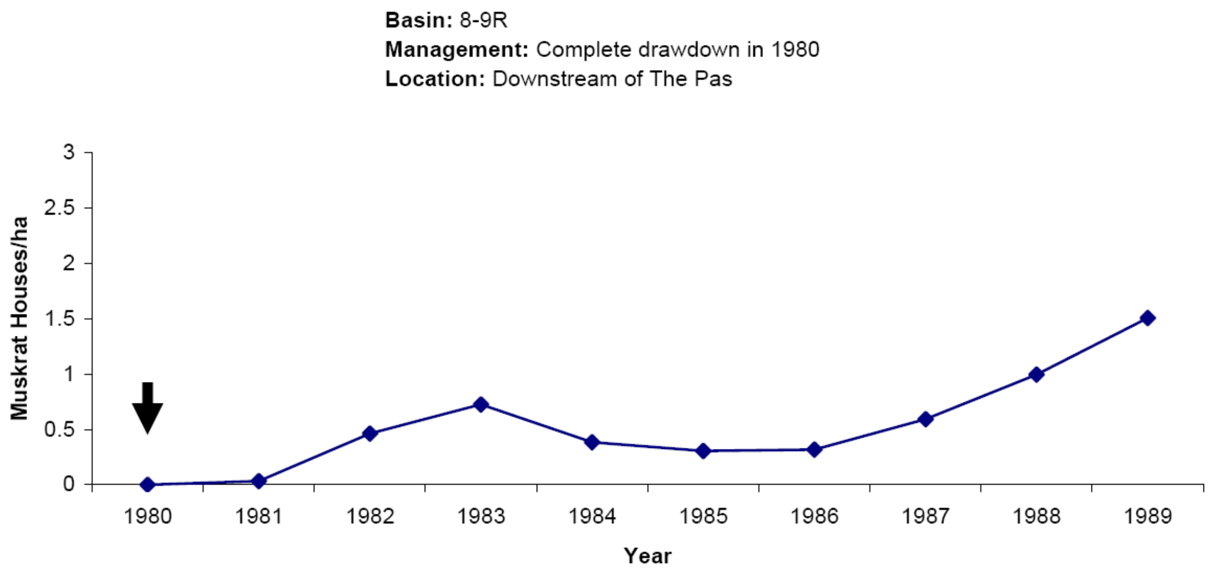


Fig. 17. Muskrat (*Ondatra zibethicus*) house counts of wetlands 8-9R from 1980-1989 in the Saskatchewan River Delta.

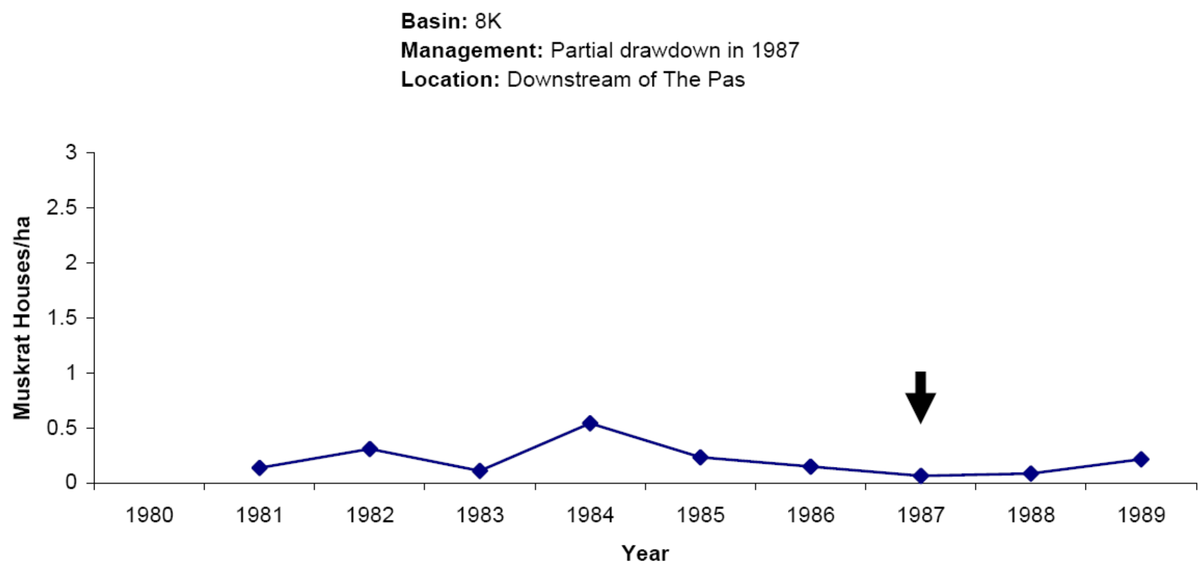


Fig. 18. Muskrat (*Ondatra zibethicus*) house counts of wetlands 8K from 1980-1989 in the Saskatchewan River Delta.

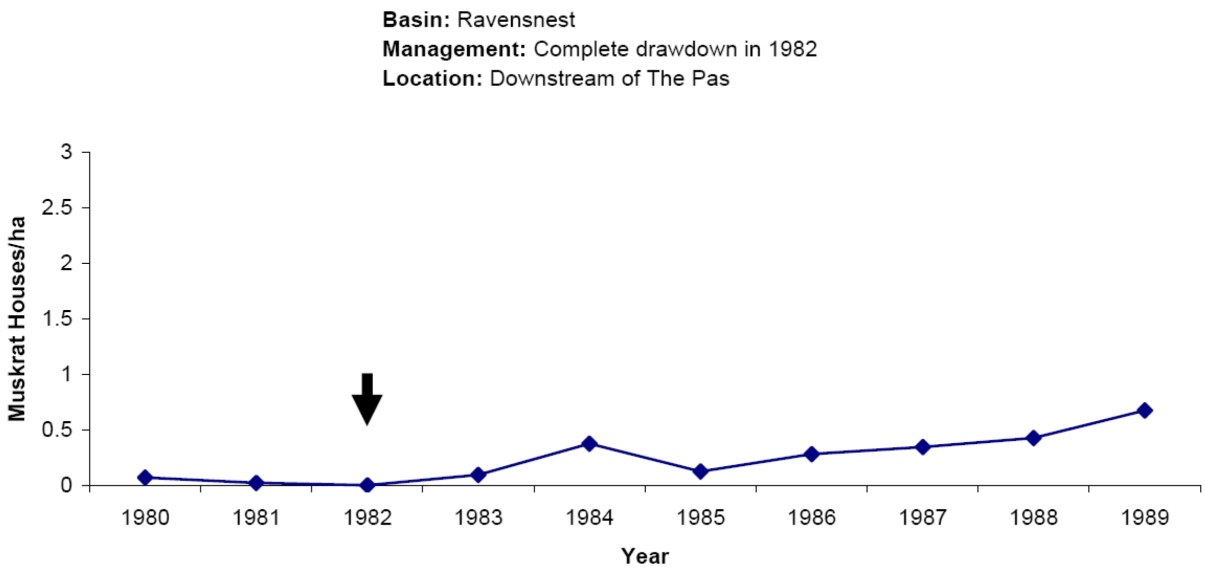


Fig. 19. Muskrat (*Ondatra zibethicus*) house counts of Ravensnest Lake from 1980-1989 in the Saskatchewan River Delta.

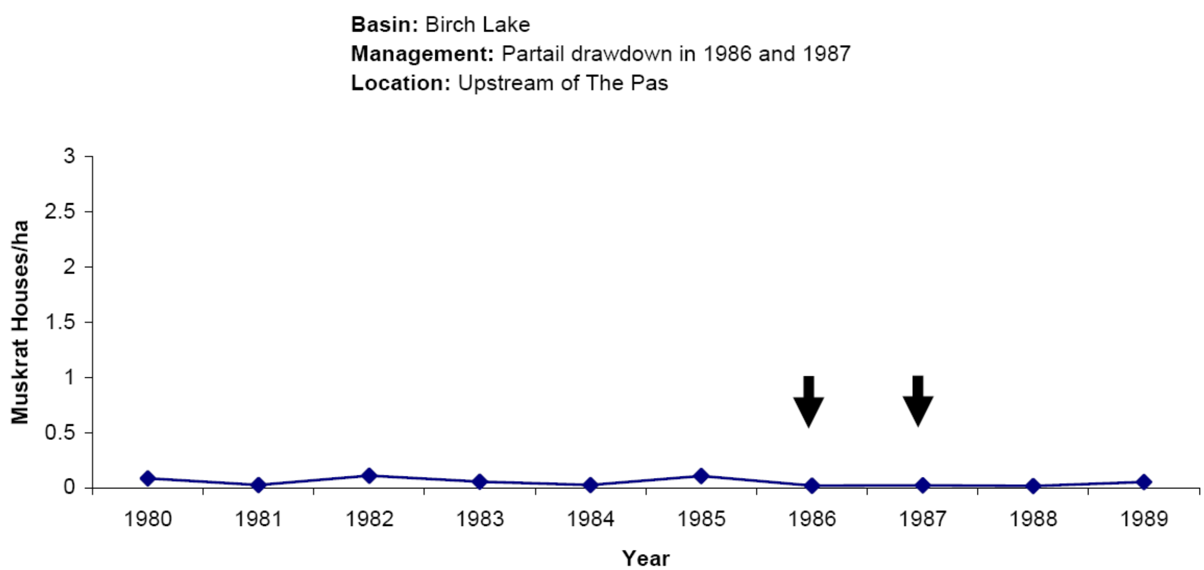


Fig. 20. Muskrat (*Ondatra zibethicus*) house counts of Birch Lake from 1980-1989 in the Saskatchewan River Delta.

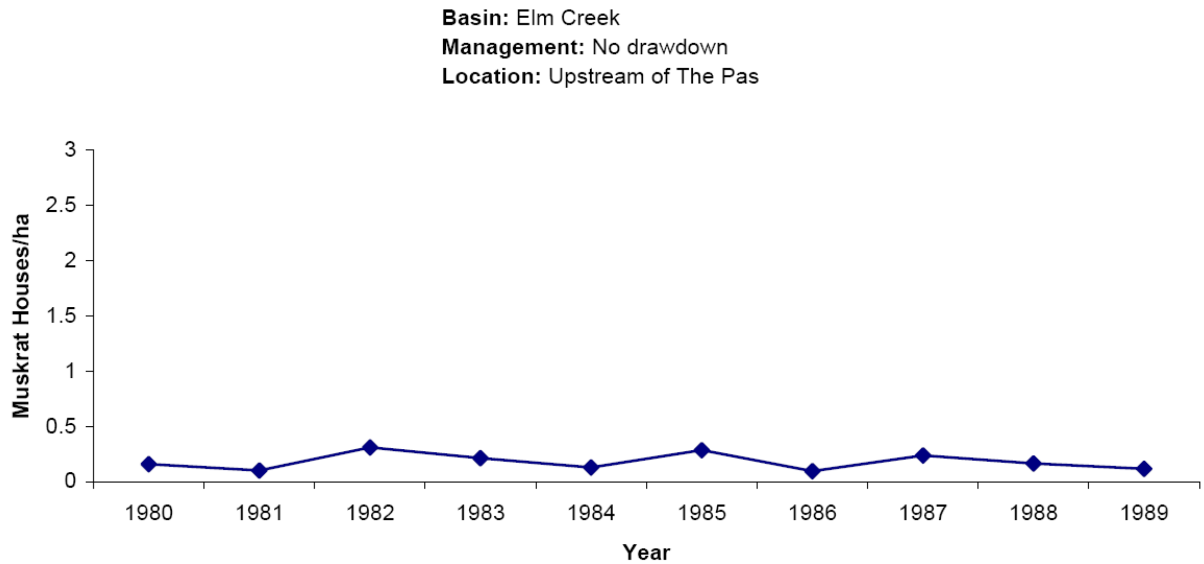


Fig. 21. Muskrat (*Ondatra zibethicus*) house counts of Elm Creek from 1980-1989 in the Saskatchewan River Delta.

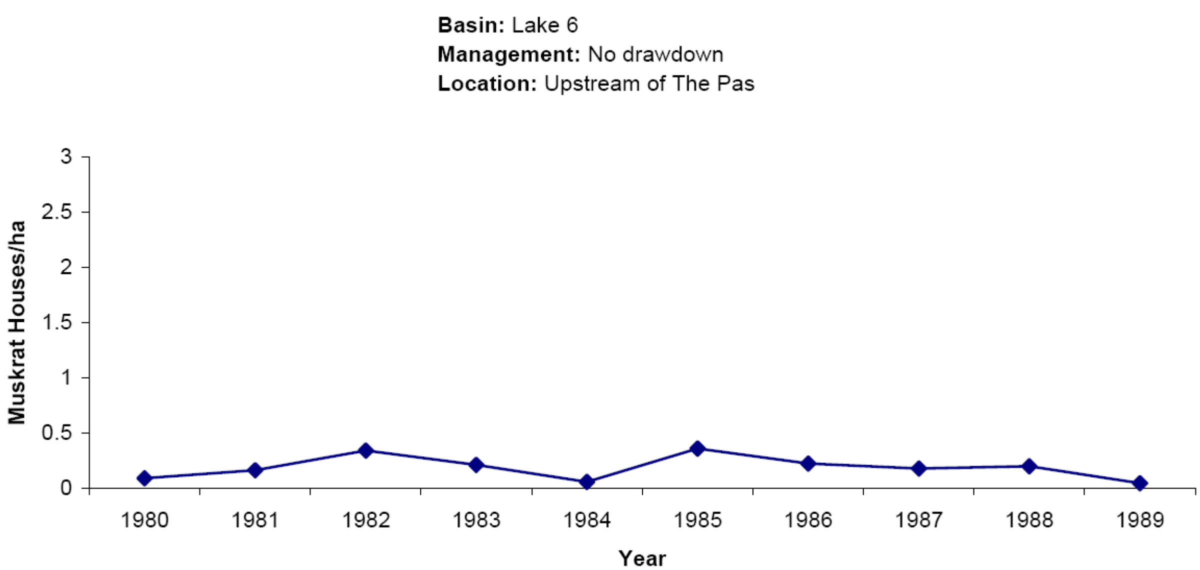


Fig. 22. Muskrat (*Ondatra zibethicus*) house counts of Lake 6 from 1980-1989 in the Saskatchewan River Delta.

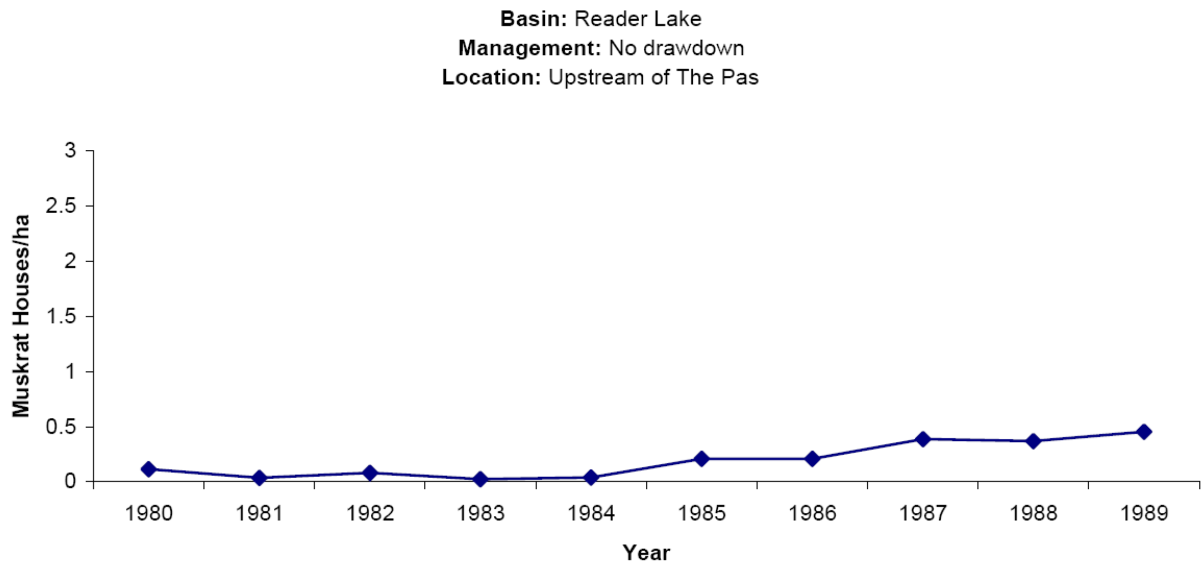


Fig. 23. Muskrat (*Ondatra zibethicus*) house counts of Reader Lake from 1980-1989 in the Saskatchewan River Delta.

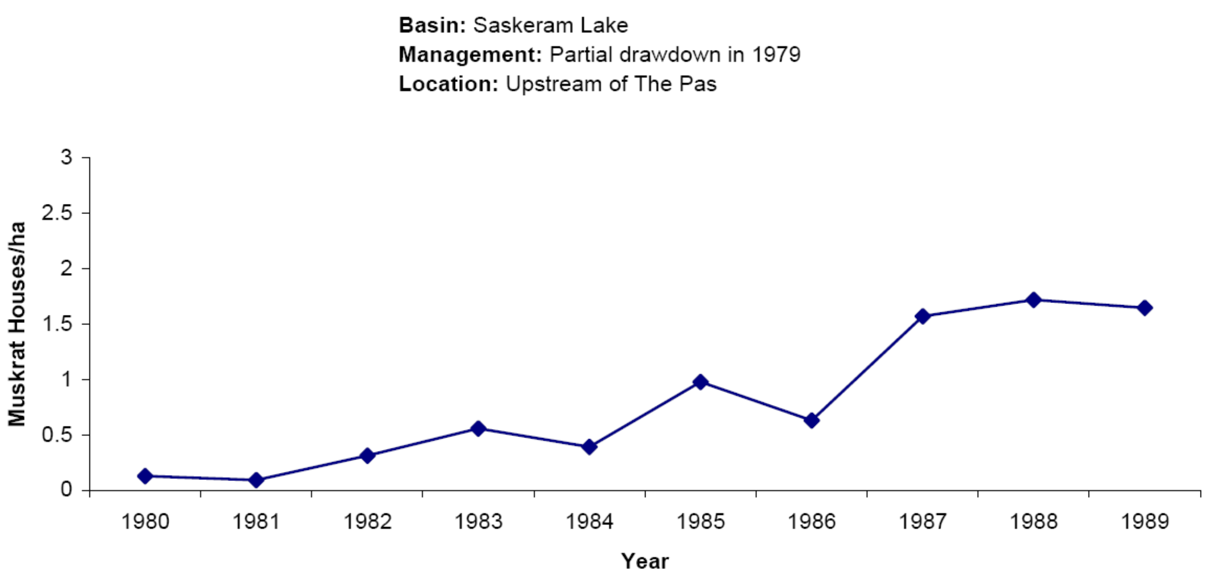


Fig. 24. Muskrat (*Ondatra zibethicus*) house counts of Saskeram Lake from 1980-1989 in the Saskatchewan River Delta.

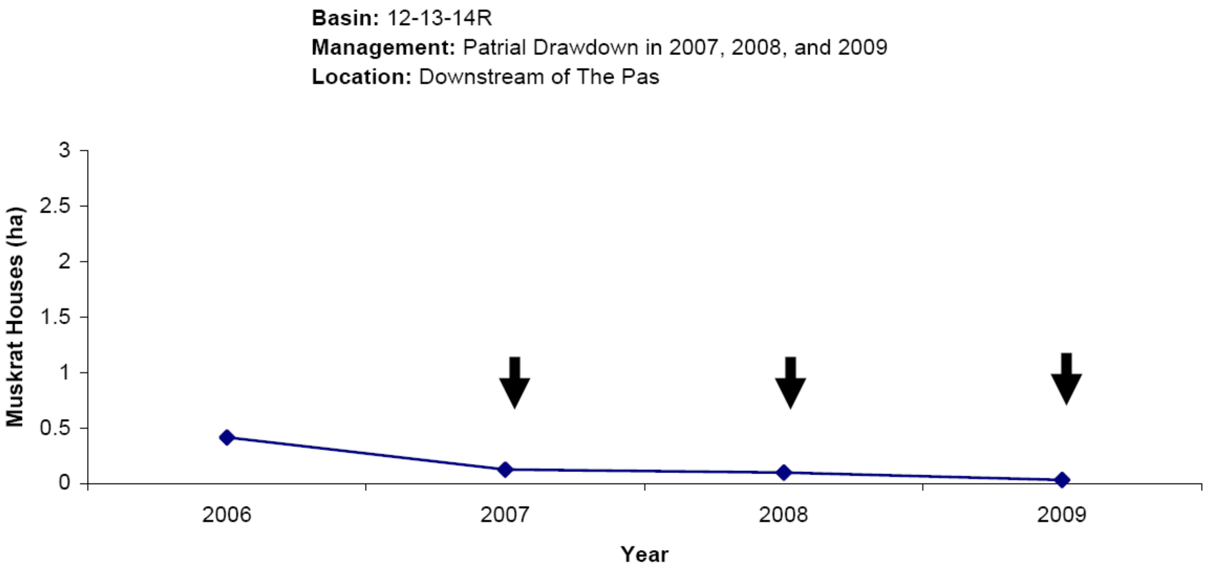


Fig. 25. Muskrat (*Ondatra zibethicus*) counts of wetlands 12-13-14R from 2006-2010 in the Saskatchewan River Delta.

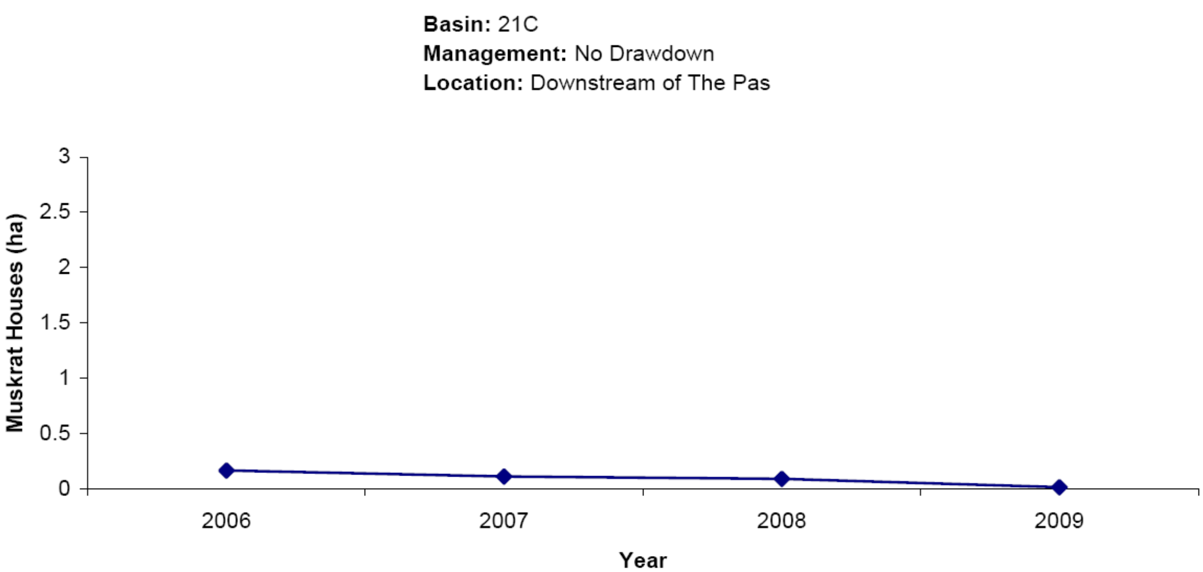


Fig. 26. Muskrat (*Ondatra zibethicus*) counts of wetland 21C from 2006-2010 in the Saskatchewan River Delta.

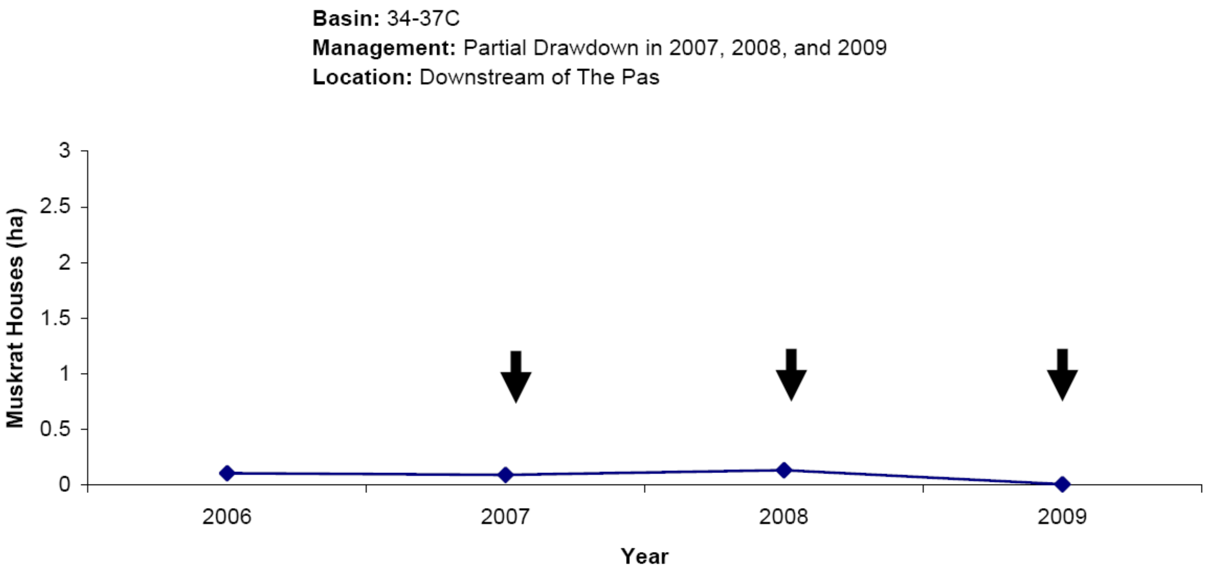


Fig. 27. Muskrat (*Ondatra zibethicus*) counts of wetlands 34-37C from 2006-2010 in the Saskatchewan River Delta.

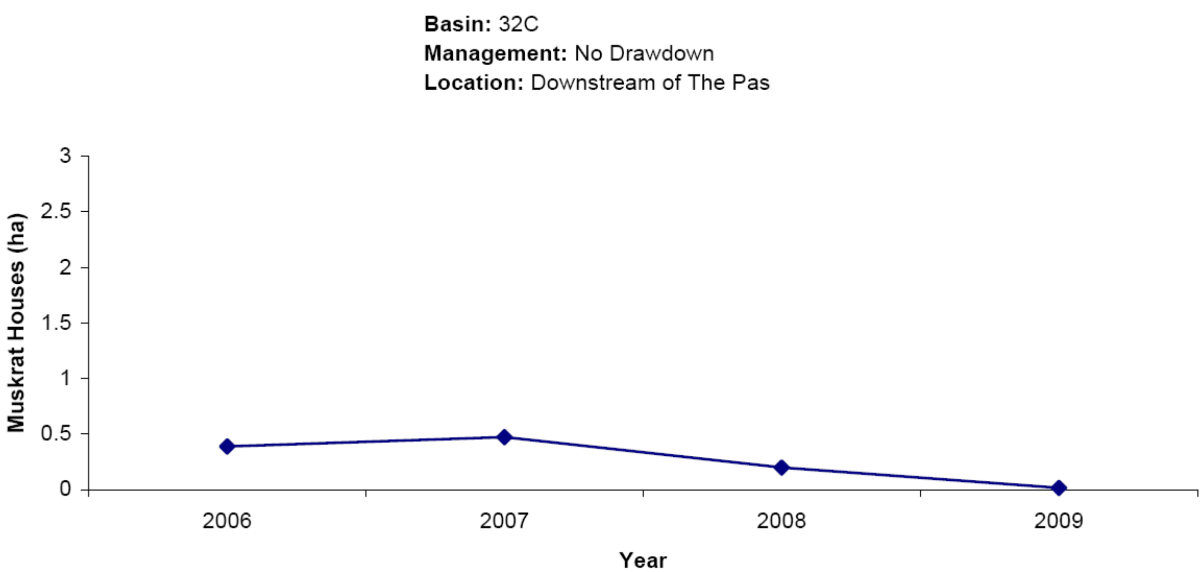


Fig. 28. Muskrat (*Ondatra zibethicus*) counts of wetland 32C from 2006-2010 in the Saskatchewan River Delta.

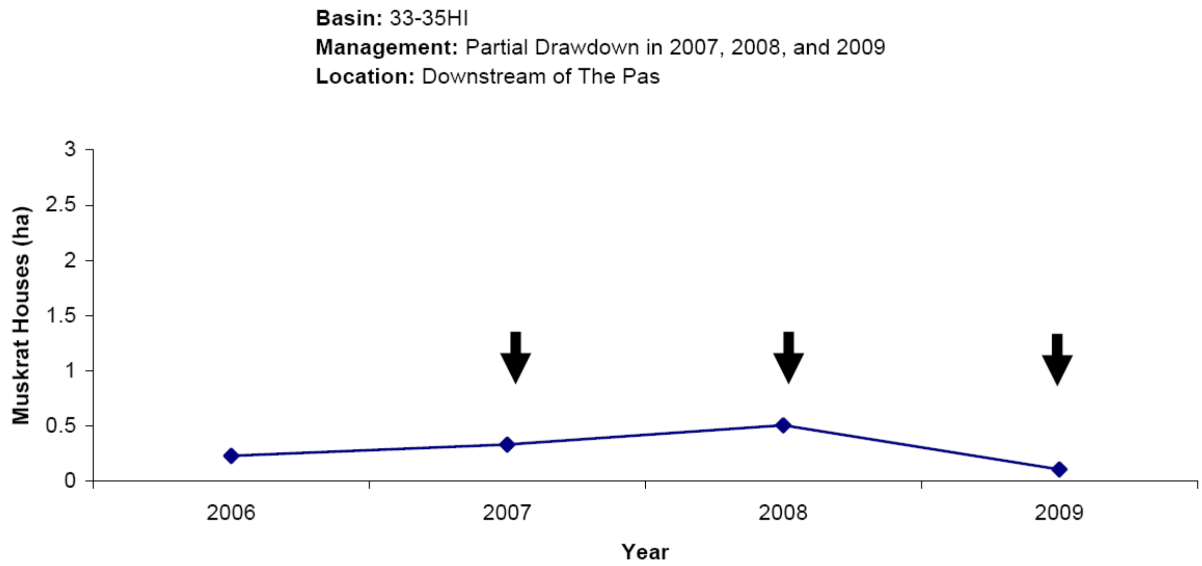


Fig. 29. Muskrat (*Ondatra zibethicus*) counts of wetlands 33-35HI from 2006-2010 in the Saskatchewan River Delta.

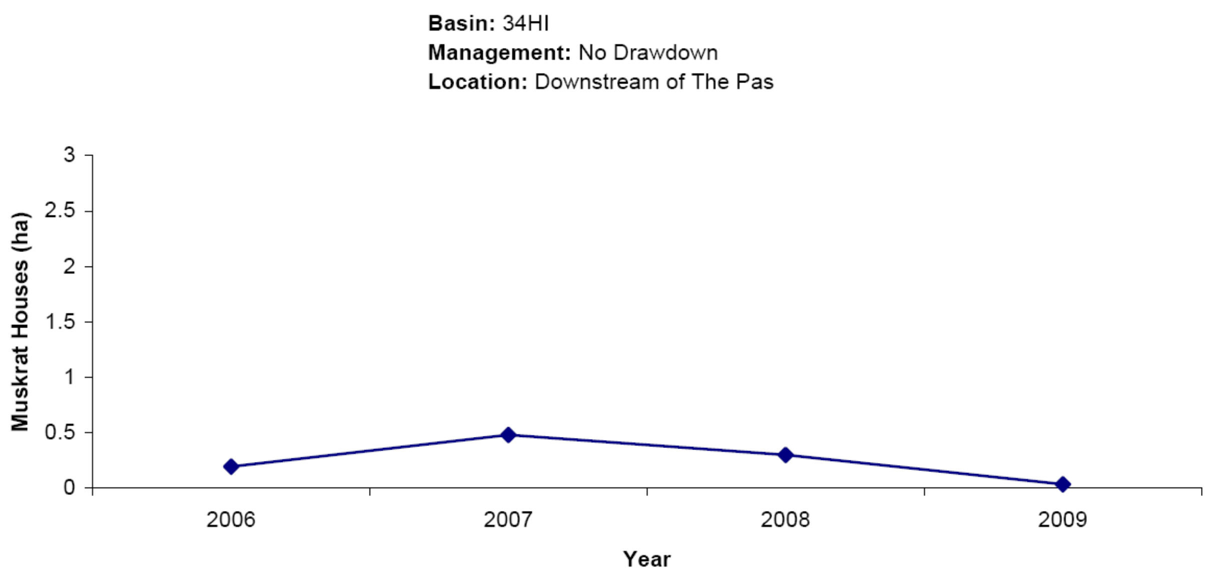


Fig. 30. Muskrat (*Ondatra zibethicus*) counts of wetland 34HI from 2006-2010 in the Saskatchewan River Delta.

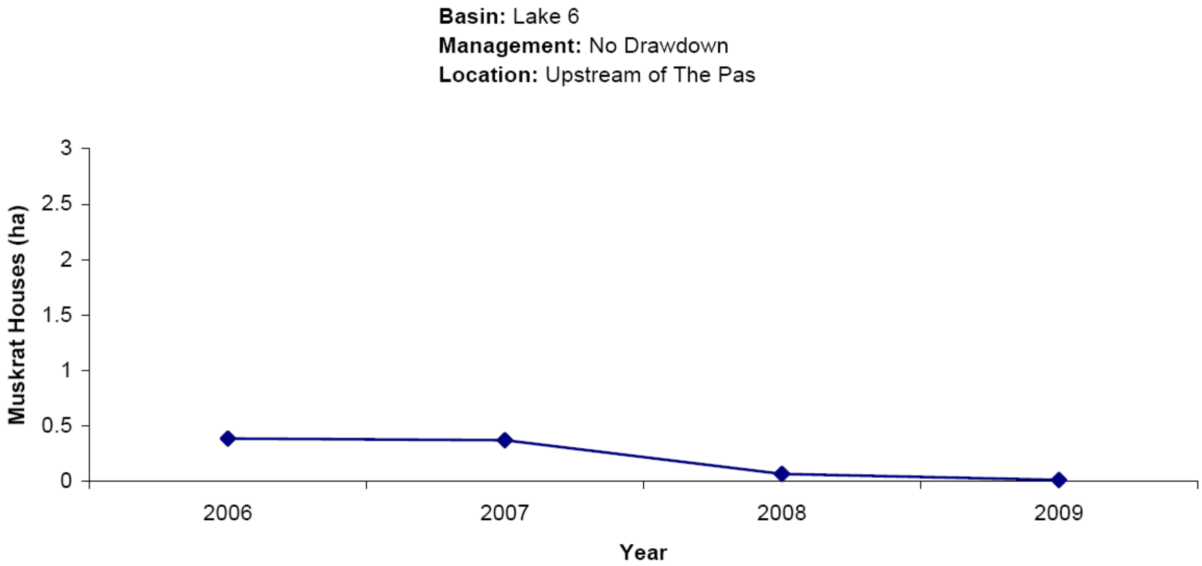


Fig. 31. Muskrat (*Ondatra zibethicus*) counts of Lake 6 from 2006-2010 in the Saskatchewan River Delta.

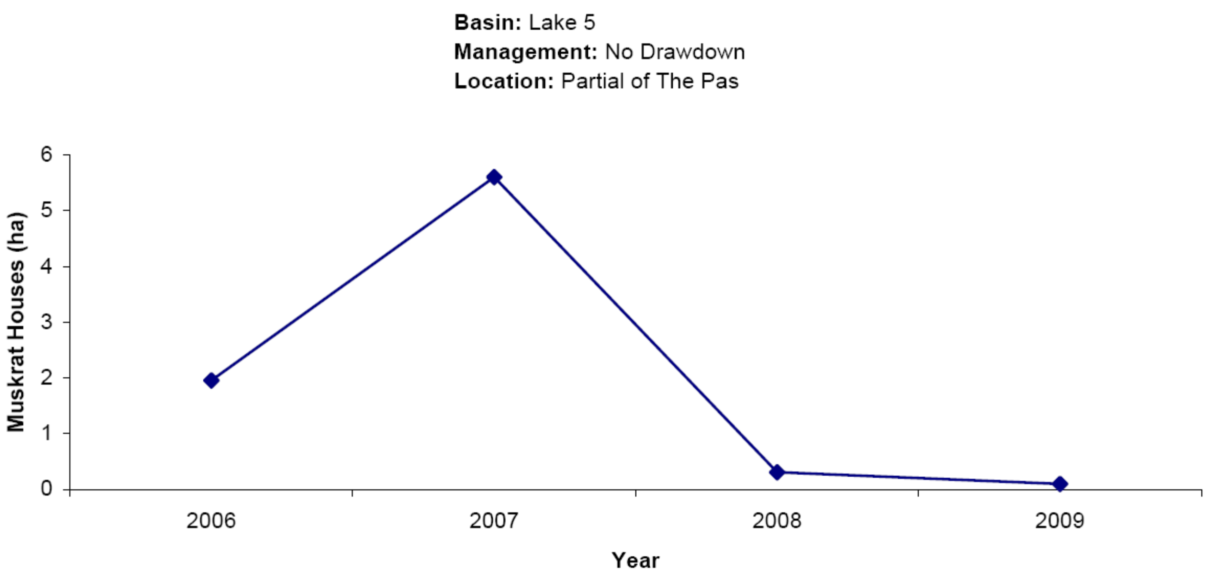


Fig. 32. Muskrat (*Ondatra zibethicus*) counts of Lake 5 from 2006-2010 in the Saskatchewan River Delta.